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BULLETIN OF THE TORREY BOTANICAL CLUB

VOL. 79, NO. 2, PP. 107–109 MARCH, 1952

PATTERNS FORMED BY MOTILE EUGLENA GRACILIS VAR. BACILLARIS[1]

WILLIAM J. ROBBINS

During experiments in which *Euglena gracilis* var. *bacillaris* was used in bioassays for vitamin B_{12}, it was noted that the organisms frequently assumed in our liquid stock cultures a distinct pattern. The pattern was composed mainly of equilateral triangles having sides about 5 mm. in length. Six of the triangles formed a well defined hexagon (fig. 1). The pattern was in the liquid not on the surface nor on the bottom of the container and was easily disturbed.

The organism was grown in 125 ml. Erlenmeyer flasks containing 25 ml. quantities of an acid medium (pH 2.5 to 2.8) of mineral salts, thiamine, glutamic acid, malic acid and 0.0001 μg. vitamin B_{12} per ml.

The formation of the pattern depended in part upon the age (or density) of the culture. The best results were obtained with cultures 5 to 9 days old. No organization was observed in cultures 1 or 2 days old; those 3 days old gave some evidence; 4 day old cultures produced fair to good patterns, and some pattern formation was observed in cultures which were a month old.

For convenience, active cultures were on occasion decanted into petri dishes 5 cm. in diameter. If the cultures contained clumps of Euglenae they were filtered through moist cheese cloth.

Organization patterns were observed in liquids varying in depth from 2 mm. to 4 cm. The most satisfactory depth was 5 or 6 mm. In a 2 mm. layer the patterns were mainly squares, 2 or 3 mm. on the side. Liquids 2 cm. or more in depth were difficult to see through.

The organization occurred quickly; within 20 to 30 seconds after the Euglenae were thoroughly dispersed and the liquid had ceased moving, definite lines of organization were visible. A complete pattern was formed within 1 minute. Viewed under a binocular microscope, the organisms appeared to swim from both sides toward the lines in which they were eventually concentrated. Although the pattern once formed was fairly constant, some of the lines could be observed to fade and re-form.

The density of the preparation appeared to be important. An active culture 6 days old containing about 2,000,000 organisms per ml., was diluted to $\frac{1}{2}$ and to $\frac{1}{4}$ strength with sterile medium. A typical pattern was formed in the culture diluted to $\frac{1}{2}$ strength, though not as quickly as in the denser preparation. A pattern was formed in the culture diluted to $\frac{1}{4}$ the original

[1] This investigation was supported in part by the Lucy Benjamin Rogers Fund and the Howard Bayne Research Fund of The New York Botanical Garden.

[THE BULLETIN for January–February (79: 1–106) was issued January 16, 1952]

strength. It was made up of patches, where the organisms were concentrated, with relatively clear areas between the patches. In some instances, the pattern suggested that the organisms were concentrated in the center of the hexagons leaving the areas between relatively clear, giving to some extent a negative of the results shown in figure 1.

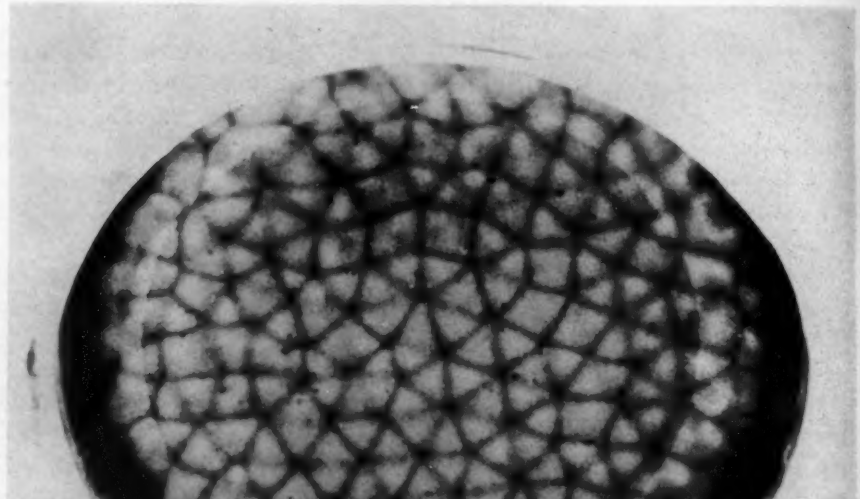

FIG. 1. Pattern formed by actively motile *Euglena gracilis* var. *bacillaris* in an acid liquid medium in a petri dish 5 cm. in diameter. Depth of liquid about 0.5 cm.

Light was not essential for the development of patterns but under some circumstances, markedly influenced the organizational response. Patterns developed in diffuse light and in darkness. Organizational activity was obtained after more than 18 hours in the dark. The formation of patterns was inhibited by sunlight; the Euglenae gathered on the bottom of the dish. It required a half hour or more for Euglenae which had been exposed to full sunlight for a few minutes, to recover the ability to form regular patterns. When the $\frac{1}{2}$ and $\frac{1}{4}$ strength preparations were strongly illuminated with artificial light from above, the patterns became unstable.

The formation of the pattern depended upon the presence of actively

motile Euglenae. Cultures in which the Euglenae were killed with a drop or two of formalin, produced no pattern. Active preparations cooled to 5 or 6° C. failed to produce a pattern, but when warmed to about 25° C. the ability to form a pattern returned.

The presence of chlorophyll was not necessary. Good patterns were obtained with 7 to 10 day old cultures of a strain which lacked chlorophyll (one produced by treating the green form with streptomycin). Cultures of the apochlorotic form which were 3 days old, gave faint evidences of pattern; those 14 days old or more, produced no pattern.

The pH of the culture medium seemed to be of significance. Dilute sodium hydroxide was added to an active preparation growing in a medium of pH 2.8. Pattern formation was still satisfactory when the medium reached pH 3.7. At 5.1, pattern formation was slow and outlines were fuzzy. At pH 6.0, very little evidence of the formation of the pattern was observed, though microscopic examination showed the Euglenae to be actively motile. The preparation was acidified with hydrochloric acid. It slowly returned to an active condition, forming good patterns after about one hour. In another preparation, the pH was raised to 8.2, where pattern formation failed to occur. It was then acidified to pH 3.3 and again slowly recovered the ability to form a typical pattern.

Patterns were obtained in 125 ml. Erlenmeyer flasks, in round petri dishes, in 8 cm. square petri dishes and in rectangular glass cells $1 \times 5 \times 5$ cm. The latter vessels were used for observations on the vertical organization. When a preparation a cm. or two deep was kept in the dark for 30 minutes, sharp lines of concentrated Euglenae extended vertically for a mm. or two below the surface; lower down these lines spread giving the appearance of a picket fence. Illumination with artificial light had little effect on the orientation in the upper two or three mm. but caused the "pickets" to spread out and lose their regularity.

It is difficult to suggest causes for the formation by actively motile Euglenae, of patterns such as are described here. The effect of pH suggests the possibility of the electrical charge being important. The effect of light deserves further investigation as some curious effects of short exposures to strong light were observed. So far as the writer is aware, a comparable phenomenon for other motile organisms has not been described.

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BULLETIN OF THE TORREY BOTANICAL CLUB

VOL. 79, NO. 2, PP. 110–125 MARCH, 1952

THE CYTOLOGY AND CROSSING BEHAVIOR OF GOSSYPIUM GOSSYPIOIDES[1]

META S. BROWN AND MARGARET Y. MENZEL

Eight American wild species of *Gossypium* are listed by Hutchinson, Silow and Stephens (1947). These include six species and a variety of one which have been studied cytologically and crossed extensively with each other and with other species, including the American cultivated species, *G. hirsutum* L. and G. *barbadense* L. The latter are amphiploid, and it has been demonstrated that one genome of the amphiploid is cytologically similar to the chromosomes of the American wild species (Webber 1935, 1939; Skovsted 1937; Beasley 1940a, 1942; Boza Barducci and Madoo 1941). Since the hypothesis of the allotetraploid origin of the American cultivated species was first proposed by Skovsted (1937), it has received support from the synthesis of an amphiploid, similar to the natural amphiploid, from an Asiatic and an American wild species by Beasley (1940b) and by Harland (1940), and from genetic data of Harland and Atteck (1941) and Silow (1946). The relationship of the American wild species to the American cultivated species has been discussed further by Stephens (1947), Hutchinson and Stephens (Hutchinson, Silow and Stephens 1947), Brown (1951) and Brown and Menzel (1950). The significance of this relationship of the wild diploids is twofold. As a consequence of their role in the origin of the amphiploid species and because of their homology with the cultivated species, the American diploids offer most promise for the introduction of desirable new characters into the highly selected varieties of *G. hirsutum* which are now in cultivation.

One of the heretofore little known American wild species is *Gossypium gossypioides* (Ulb.) Stanley; it has been placed with *G. thurberi* in the Section Thurberana by Hutchinson (Hutchinson, Silow and Stephens 1947) on the basis of geographical and morphological data. Since complex trispecies hybrids involving *G. thurberi,* the Asiatic cultivated diploid *G. arborem,* and *G. hirsutum* have been used in breeding experiments, it is of particular interest to compare the cytological and crossing behavior of *G. gossypioides* with that of *G. thurberi* and other members of the wild American species.

[1] Contribution No. 1481 from Department of Agronomy, Cotton Investigations Section, Texas Agricultural Experiment Station, College Station, Texas. Part of the work was done under Regional Cotton Genetics Project S-1 of the Research and Marketing Act of 1946.

Materials and methods. Following the terminology of Beasley (1940a, 1942) and Brown and Menzel (1950), the following symbols will be used to designate the genomes of *Gossypium* species:

G. herbaceum	A_1
G. arboreum	A_2
G. anomalum	B_1
G. sturtii	C_1
G. thurberi	D_1
G. armourianum	$D_{2\text{-}1}$
G. harknessii	$D_{2\text{-}2}$
G. klotzschianum	$D_{3\text{-}k}$
G. klotzschianum var. *davidsonii*	$D_{3\text{-}d}$
G. aridum	D_4
G. raimondii	D_5
G. gossypioides	D_6
G. stocksii	E_1
G. hirsutum	$(AD)_1$
G. barbadense	$(AD)_2$
G. hirsutum subgenomes	A_h, D_h

In January, 1946, a collecting trip was made to Central and Southern Mexico by T. R. Richmond and C. W. Manning, of the Agronomy Department of the Texas Agricultural Experiment Station, to find new species and strains of *Gossypium*. Included among the introductions made as a result of this expedition were two collections[2] of a diploid species identified as *Gossypium gossypioides* (Ulb.) Stanley and confirmed by J. B. Hutchinson.

Seeds were collected from two areas, 60 and 83 miles south of Oaxaca, Mexico. The plants were growing wild under semi-arid conditions on a well drained, rocky, calcareous soil. The shrubs were 5 to 6 feet high, with flowers and bolls. The midwinter flowering and fruiting season of *G. gossypioides* coincided with that of short-day species, and it has consistently exhibited short-day periodicity in greenhouse culture, flowering from mid-October to late April.

The description of *G. gossypioides* as found in the wild and in greenhouse culture agrees with that given by Hutchinson, Silow and Stephens (1947). Additional description is as follows: Plants may reach a height of 10 to 12 feet in the greenhouse when planted in large pots with some roots extending into the soil. Leaves are usually 3-lobed, sometimes 5-lobed. The nectary on the midrib is vestigial and not apparent to the unaided eye. The extrafloral nectaries at the base of the calyx are often empty. The

[2] P. I. 154005, C. B. 1754 and P. I. 154007, C. B. 1756.

nectaries outside the bracteoles, commonly found in many other species, are absent in *G. gossypioides*. The edges of the bracteoles are adherent until the day of flowering, and closely invest the flower and boll (fig. 2). Flowers are large, about 5 cm. long and 5 to 8 cm. across. The petal color varies from pink to almost white, with a rose flush on the outer margin. There is a large deep red petal spot covering most of the lower half of the petal (fig. 1). *G. gossypioides* resembles *G. raimondii* in having also a small

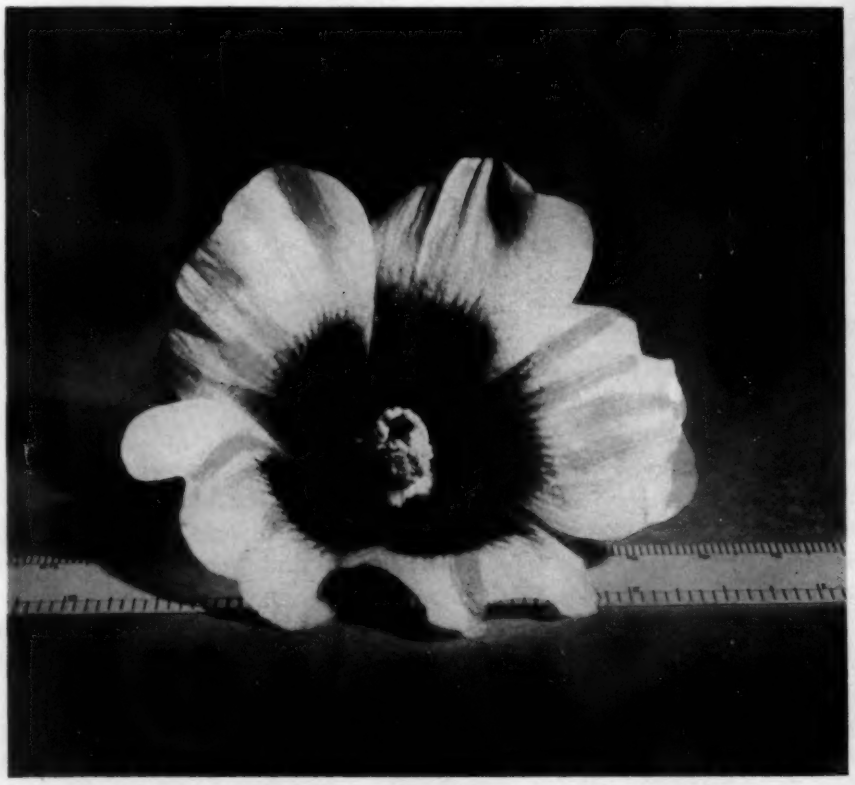

FIG. 1. Flower of *Gossypium gossypioides*, showing the large petal spot.

red spot near the base on the *outside* of the petal (reverse petal spot). The staminal column is separated into five sections, with many short, compactly arranged filaments (fig. 2). The style is long and slender, the ovary small with few ovules. Bolls usually have 3, sometimes 4 locules. Mature bolls open widely, exposing 1 or 2, rarely as many as four, seeds per locule. Seed hairs are buff colored and about 1 cm. in length. Bolls fall intact with bracteoles soon after maturity, abscission occurring at the base of the peduncle.

Results. Crossing behavior of G. gossypioides. The crossing behavior of *G. gossypioides* has been tested with 11 diploid and one tetraploid

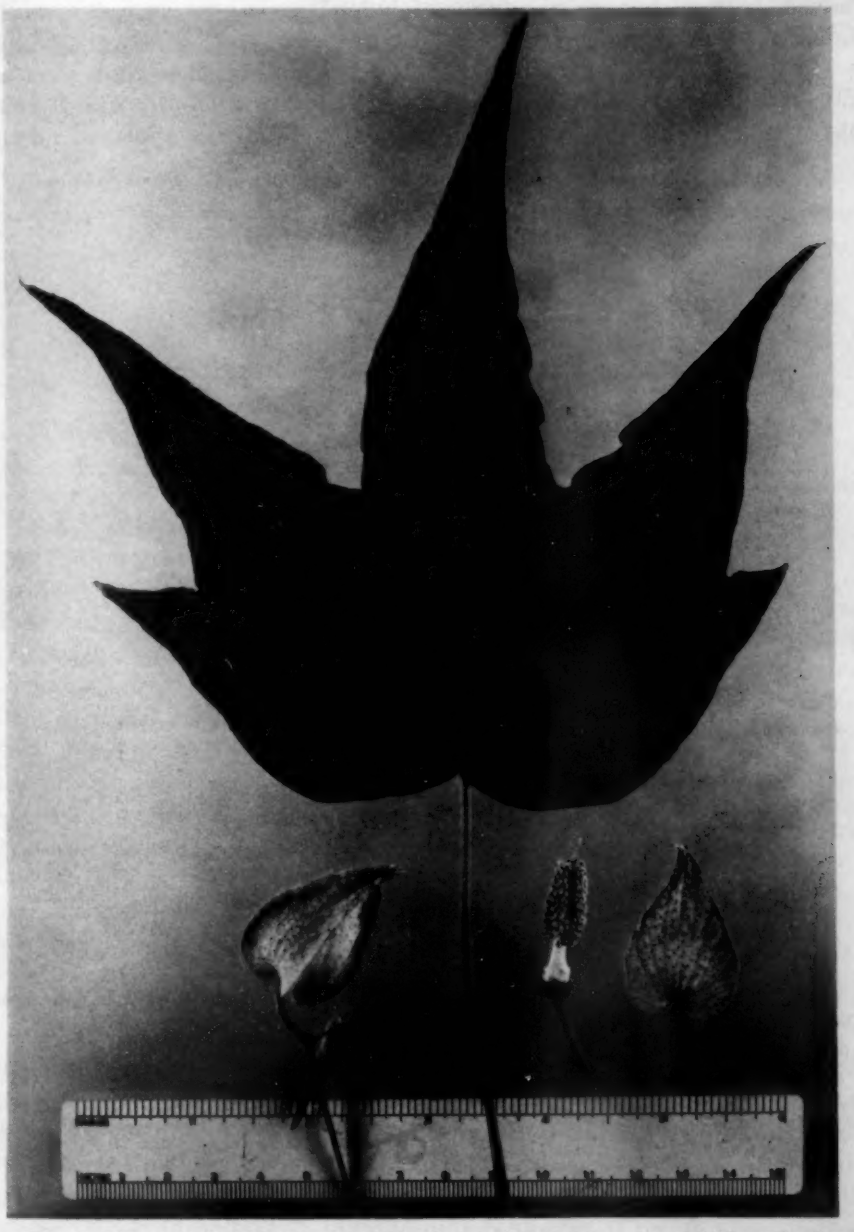

FIG. 2. Climax leaf, bud and staminal column of *Gossypium gossypioides*. The bracteoles are adherent in the bud. Note the separation of the staminal column into sections.

species. Crosses have also been attempted with 14 different synthesized amphiploids, 6 tetraploid and 8 hexaploid. Table 1 shows the results obtained. In most instances embryos of hybrid seeds were excised and germinated on nutrient agar.

Hybrids with *G. herbaceum*, *G. arboreum* and *G. anomalum* were obtained, although some bolls fall and most seeds are empty. The hybrids listed in Table 1 lived from 2½ to 4 months. Seedlings appeared normal

TABLE 1. *Crosses between G. gossypioides and other species and hybrids*

	Number of flowers pollinated	Number of bolls harvested	Number of seeds harvested	Number of seeds germinated on agar	Number of selfs	Number died in cotyledon stage	Number of seeds dissected	Number of seeds empty	Number of hybrids obtained	Remarks
Diploid species										
$A_1 \times D_6$	16	11	136	65	63	2			2	One hybrid lived 2½ months
$A_2 \times D_6$	79	41	many	122	103	19	9	9	1	Hybrid lived 3–4 months
$B_1 \times D_6$*	13+	13	102	28	27	1			1	Hybrid slow-growing; lived 3–4 months
$D_1 \times D_6 + S$**	30+	30	many	26	4	22	14	8		
$D_6 \times D_1$*	28+	3	7	7		7	1	6		
$D_{2-2} \times D_6$*	19	2	2	1				1		
$D_6 \times D_{2-2}$	23	4	18	9		9		9		Cotyledons not green, not expanded
$D_{2-4} \times D_6$	3	1	18	10		10	5	5		
$D_5 \times D_6$	20	2	17				2			7 seeds planted in soil
$D_6 \times D_5$	44	6	23	10	4	6		6		Cotyledons not expanded, green or non-green
Tetraploid species and hybrids										
$4A_2 \times D_6$	2	2	26	7	2	5			5	One hybrid lived 7 months
$2A_2B_1 \times D_6$	26	10	46	8			2	5	1	Hybrid lived 4–5 months
$2A_2D_1 \times D_6$	84	3	22	16	16					
$2A_2E_1 \times D_6$*	9	6	51							12 seeds planted in soil
$2(AD)_1 \times D_6$	18	18	107	22		22			22	Hybrids lived 3–9 months

* Some pollinations made plus self; not all recorded.

** D_1 always used without emasculation as female because emasculated flowers are shed almost immediately.

until two or three leaves developed, then growth ceased, and the plants eventually died without flowering.

Hybrids with species of the American wild group were not obtained or died in the cotyledon stage. Cotyledons of possible hybrids with *G. thurberi*, *G. harknessii* and *G. raimondii*, excised and placed on agar, remained non-green or failed to expand despite normal elongation of the hypocotyl. Positive verification of the hybrid constitution could not be made in such

cases. In addition to the seeds excised, 15 seeds of this cross were planted in soil. The five which germinated were selfs of *G. thurberi*. Of seven seeds of the cross *G. raimondii* × *G. gossypioides*, six germinated giving two selfs. Of the reciprocal cross, nine seeds planted in soil gave two selfs.

In addition to the crosses listed in Table 1, the following pollinations with diploid species were made:

Female		Male	Number	Reciprocal crosses Female		Male	Number
D_6	×	A_1	9	C_1	×	D_6	1
"	×	A_2	11	$D_{2\text{-}1}$	×	"	3
"	×	B_1	38	$D_{3\text{-}k}$	×	"	3
"	×	C_1	5	E_1	×	"	2
"	×	$D_{2\text{-}1}$	1				
"	×	$D_{3\text{-}k}$	22				
"	×	$D_{3\text{-}d}$	12				
"	×	E_1	34				

No bolls were harvested from any of these crosses. At least three selfed bolls of *G. gossypioides*, two with as many as four seeds in a locule, have been harvested from hand pollinated previously emasculated flowers. The early falling of outcrossed *G. gossypioides* flowers is therefore not due to emasculation alone, as seems to be the case in *G. thurberi*.

G. gossypioides crosses readily when used as pollen parent with tetraploids, both natural and synthesized. It can be crossed rather easily with tetraploid *G. arboreum*, doubled *herbaceum-arboreum* and doubled *arboreum-anomalum*. Hybrids of tetraploid *G. arboreum* × *G. gossypioides* and of doubled *arboreum-anomalum* × *G. gossypioides* have survived several months, but growth is slow and plants die without forming buds or flowers. No plants obtained from 15 seeds of the latter cross lived long enough to graft to normal stock. One boll, with 9 seeds, was harvested following pollination of 11 flowers of doubled *herbaceum-arboreum*. Crossed bolls on doubled *arboreum-thurberi* usually fall after two to four weeks. Three mature bolls with one good seed and many empty seeds have been harvested from this cross. Bolls on doubled *arboreum-stocksii* may mature but of 12 seeds planted in soil only three germinated. One of these died in the cotyledon stage; the other two are apparently selfs. No bolls have been obtained from 12 flowers of doubled *davidsonii-anomalum* crossed with *G. gossypioides*. Nine flowers of the F_1 hybrid of *thurberi-raimondii* pollinated with *G. gossypioides* fell within a few days after pollination, as did 8 flowers of the reciprocal cross.

Crosses with *G. hirsutum* are easily made. Few bolls fall, and although the harvested bolls contain only 2 to 12 large seeds per boll, most of these large seeds germinate readily and all seedlings are hybrids. Seedlings appear normal at first, but at about the time of onset of bud formation,

growth is retarded, and the leaves become markedly epinastic, with discolored, leathery, cupped under blades (fig. 3). Stems become brittle and are streaked internally with brown necrotic areas. Plants often bloom profusely just before dying but may live 3 to 6 months before all tissue is dead. Grafting of F_1 hybrid scions to normal *hirsutum* does not prevent or delay the morbid symptoms. One hybrid seedling and a grafted scion from it were both discarded in similar condition after 9 months.

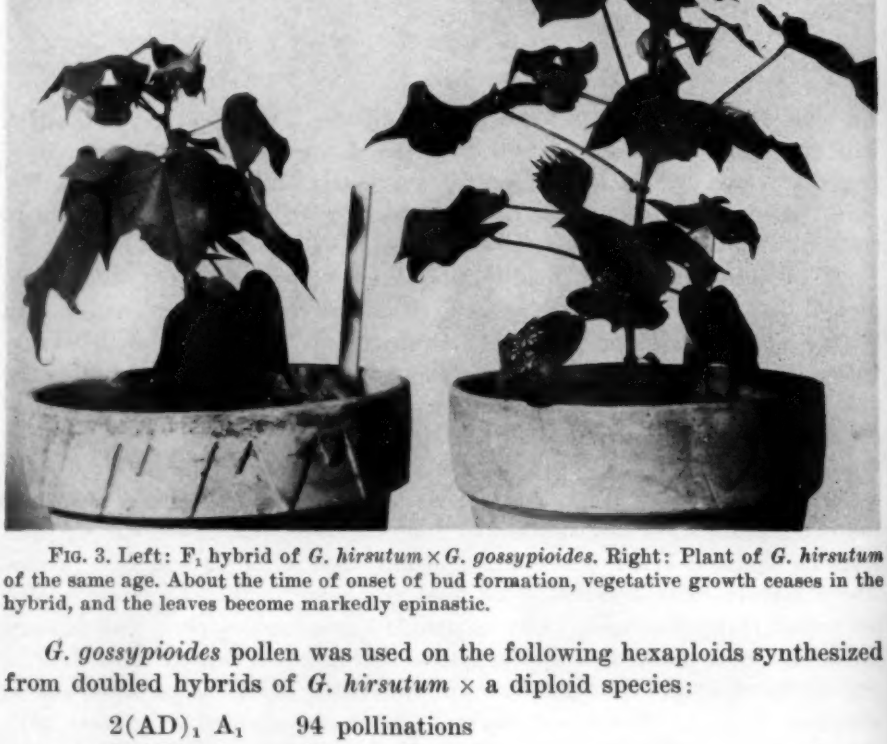

FIG. 3. Left: F_1 hybrid of *G. hirsutum* × *G. gossypioides*. Right: Plant of *G. hirsutum* of the same age. About the time of onset of bud formation, vegetative growth ceases in the hybrid, and the leaves become markedly epinastic.

G. gossypioides pollen was used on the following hexaploids synthesized from doubled hybrids of *G. hirsutum* × a diploid species:

$2(AD)_1$ A_1	94	pollinations
$2(AD)_1$ A_2	49	"
$2(AD)_1$ B_1	35	"
$2(AD)_1$ C_1	14	"
$2(AD)_1$ D_1	12	"
$2(AD)_1$ $D_{2\text{-}1}$	18	"
$2(AD)_1$ D_5	16	"
$2(AD)_1$ E_1	72	"

No bolls were harvested from any of these hexaploids. One or more of these hexaploids, involving the diploid species *G. herbaceum, G. arboreum, G. anomalum* and *G. stocksii,* have been crossed with other members of the American wild species, including *G. armourianum, G. harknessii* and *G. raimondii* (Brown and Menzel 1950), so that failure of hexaploid × *G. gossypioides* crosses cannot be due entirely to a general incompatibility of diploid pollen in hexaploid styles.

When hexaploids are pollinated with *G. gossypioides* pollen, most flowers fall in several days, but on *hirsutum-herbaceum* hexaploids young bolls may remain on the plant 3 or 4 weeks or longer. The period between anthesis and harvest of selfed or other normally developing bolls averages about 8 weeks in *G. hirsutum;* embryos reach their maximum size within approximately 4 weeks (Reeves and Beasley 1935), and Lofland (1950) was able to culture embryos 27 days old or older on artificial medium. When *G. thurberi* and *G. raimondii* are crossed onto the hexaploid *hirsutum-arboreum,* most bolls fall, as in the *gossypioides* cross, but after many attempts tetraploid hybrids of the first two crosses have been obtained. J. R. Meyer (unpublished data) obtained both hybrids from culture of immature embryos. The second tetraploid, $(AD)_1A_2D_5$, has subsequently been obtained by the authors from a single large seed of a mature boll planted directly in soil. This hybrid has also been obtained by S. G. Stephens (unpublished data).

A total of 36 reciprocal crosses has been attempted with pollen from five of the above hexaploids on *G. gossypioides* without success.

Cytology of G. gossypioides and F_1 G. hirsutum × G. gossypioides. At metaphase I of *G. gossypioides* 13 bivalents are present (fig. 4), as in all other wild species of cotton (excepting the amphiploid *G. tomentosum*); the species is therefore a diploid as expected. Bivalents usually have 2 chiasmata, although as many as 6 one-chiasma bivalents were found in a single cell.

Meiosis has been studied in two F_1 plants of *G. hirsutum* × *G. gossypioides.* Chromosomes of *G. gossypioides* pair with the smaller chromosomes of *G. hirsutum* (figs. 5–7) as do those of all other American wild species which have been studied. In table 2 is given the detailed count of 39 plates, showing a range of 8–13 bivalents, 0–3 trivalents, and 12–21 univalents. Nine additional cells in which one univalent was unaccounted for showed the same range of pairing. The pairing found in the F_1 hybrids of *G. hirsutum* × *G. gossypioides* confirms the assumption that *G. gossypioides* is a member of the D genome species, following Beasley's (1942) classification. In table 3 are given the mean number of bivalents, univalents, trivalents and quadrivalents found in a series of F_1 hybrids involving *G. hirsutum* or *G. barbadense* and members of the D genome species. Inspection of the

table shows that the average pairing of *G. gossypioides* with *G. hirsutum* is very near the range of that of other American wild diploids.

Most of the trivalents in the F_1 hybrid of *G. hirsutum* × *G. gossypioides* appear to be ADD, involving one large and two small chromosomes (fig. 6). Trivalents in the F_1 were frequently formed of a small two-chiasma

FIG. 4. Metaphase I in PMC of *G. gossypioides*, showing 13 II. FIG. 5–7. Metaphase I in PMC of *G. hirsutum* × *G. gossypioides*. FIG. 5. 11 II, 13 large and 4 small I. FIG. 6. 11 II, 1 III, 14 I. The trivalent is composed of 2 small and 1 large chromosome. FIG. 7. 13 small II, 13 larger I.

bivalent with a large chromosome attached. The number of trivalents in this F_1 hybrid, as in other hybrids involving the D genome species, is less than the number of bivalents in haploids of *G. hirsutum*. Beasley (1942) found a mean of 1.7 bivalents in 66 cells of such haploids. In table 4 are additional data on the pairing in haploid *G. hirsutum* showing a range of 0–6 bivalents in 70 cells, with a mean of 1.35. The bivalents almost invari-

TABLE 2. *Meiotic pairing in F_1 hybrids of G. hirsutum × G. gossypioides*

II	III	I	Number of pollen mother cells		
			Plant No.1	Plant No. 2	Total
13		13	3	3	6
12	1	12	2	1	3
12		15	3	6	9
11	1	14	5	1	6
11		17	2	3	5
10	2	13	–	1	1
10	1	16	–	2	2
10		19	1	3	4
9		21	–	1	1
8	3	14	1	–	1
8	2	17	–	1	1
Total 438	18	591	17	22	39
Average 11.23	0.46	15.15			

TABLE 3. *Summary of average pairing in (AD)D hybrids*

Genome Composition	Average number of				Authority	
	II	III	IV	I		
$(AD)_1D_1$	12.45	0.2		13.5	Skovsted	1937
" "	12.05	0.5		13.4	"	"
$(AD)_2D_1$	12.04	0.5		12.7	"	"
$(AD)_1D_1$	12.70	0.18		13.06	Webber	1939
$(AD)_2D_1$	12.67	0.13		13.27	Ivengar	1944
$(AD)_1D_{2-1}$	12.15	0.4		13.5	Skovsted	1937
" "	13.35	0.15		11.85	"	"
" "	12.7	0.05		13.45	"	"
" "	12.1	0.10		14.5	"	"
$(AD)_2D_{2-1}$	12.05	0.05		14.75	"	"
" "	12.0	0.6		13.2	"	"
$(AD)_1D_4$	12.4	0.35		13.15	"	"
" "	12.0	0.6	0.05	13.0	"	"
$(AD)_2D_4$	12.28	0.15		13.99	"	"
$(AD)_1D_5$	11.65	0.87	0.125	12.57	Boza Barducci and Madoo	1941
$(AD)_1D_6$	11.23	0.46		15.15	Authors	

TABLE 4. *Meiotic pairing in haploids of G. hirsutum*

	Number of		Number of
	II	I	PMC
	6	14	1
	4	18	4
	3	20	8
	2	22	20
	1	24	19
		26	18
Total	105	1610	70
Average	1.5	23.0	

ably have only one chiasma, and are often obviously asymmetrical, indicating intergenomic pairing between A and D genomes. It is thus not necessary to assume any intragenomic pairing, either within the A_h, D_h or D_n genomes, to explain the relatively few trivalents found in the triploid F_1 hybrids.

Discussion. The relationship of G. gossypioides to other species. The geographical location of *G. gossypioides* places it categorically among the American wild species. Despite the failure to obtain verified hybrids with other members of this group, the small size of the chromosomes, and their behavior in the F_1 hybrid with *G. hirsutum*, confirm *G. gossypioides* as one of the D genome species. Its relationship within this group is further clarified by consideration of its crossing behavior and its morphological characters.

G. gossypioides has been placed in the Section Thurberana by Hutchinson primarily on morphological grounds. In some respects, however, *G. gossypioides* is no more similar to *G. thurberi* than to certain other American wild species, for example, *G. raimondii*. In flower size, shape and color, and in leaf shape and stem texture, *G. gossypioides* is intermediate between *G. thurberi* and *G. raimondii*. It has, in fact, a marked superficial resemblance to the F_1 hybrid of the latter two species. In this hybrid, the intermediate expression of all divergent characters, which is characteristic of *Gossypium* hybrids, is very striking. The flower of *G. thurberi* is a relatively small, open, shallow cup; that of *G. raimondii* is very large, and narrowly campanulate. The flower of *G. gossypioides* is medium large, and open campanulate. In *G. thurberi* the filaments are loosely arranged, of medium length; in *G. gossypioides* they are short and numerous, forming a compact staminal column, sharply divided into five sections as in *G. raimondii*. The red filaments and large petal spot of *G. gossypioides*, as well as the small reverse petal spot, likewise suggest *G. raimondii*, rather than *G. thurberi*, which has white filaments and a small pink petal spot of low penetrance in hybrids. In leaf texture, *G. gossypioides* is more like *G. thurberi* than like *G. raimondii*, which is markedly tomentose; but the stems and petioles of *G. gossypioides*, unlike those of *G. thurberi*, are very minutely tomentose, much more so than in the F_1 *thurberi-raimondii* hybrid and only slightly less tomentose than in *G. raimondii* itself.

Characters which cannot be fitted into the above comparison are the bracteoles, which are unlike in all three species; and the leaf nectaries, which are functional in both *G. thurberi* and *G. raimondii* but vestigial in *G. gossypioides*. Hutchinson has pointed out that *G. thurberi* and *G. gossypioides* have many-jointed fruiting branches in common; in *G. raimondii* they are 1- or 2-jointed. Although *G. gossypioides*, like *G. thurberi*, has numerous flowers on each fruiting branch, many flowers are shed,

even under favorable growing conditions; and the percentage of open pollinated bolls as well as the number of seeds per boll is much lower in *G. gossypioides.*

Further conclusions regarding the relationship of these three species can be drawn from their crossing behavior. The D genome includes more species than any other group. Each of these species (disregarding for the moment *G. gossypioides*) has been crossed with one or more other species of the D group. However, many crosses can be made in one direction only. Furthermore, the D_3 species has a factor for incompatibility such that crosses with all other D species produce either empty seeds only, or hybrids which die in the cotyledon stage. Actually, the only viable hybrids which have been reported within the D group (with the exception of crosses between the two D_2 species, *G. armourianum* and *G. harknessii,* and between *G. klotzschianum* and its geographically isolated variety *davidsonii*) are the following:

$D_1 \times D_4$
$D_1 \times D_5$
$D_{2\text{-}1}$ and $D_{2\text{-}2} \times D_1$ and
$D_{2\text{-}1} \times D_4$

It is evident that crossing barriers have arisen between many of these species with little or no change in their cytological relationship. Hybrids between two D species which have been studied cytologically show little chromosome differentiation, and any two D species show the same type and degree of pairing when crossed with a third species, such as *G. hirsutum.*

It is apparent, therefore, that the ability or failure to cross cannot alone be regarded as a valid criterion for establishing relationships between species within the D genome. The failure to obtain viable hybrids between *G. gossypioides* and other members of the D genome group is not an exceptional circumstance. The crossing behavior of *G. gossypioides* with other D species thus tells us little of its relationship to these species, except to indicate that its relationship to *G. thurberi* is less close than its inclusion in the Section Thurberana might have indicated. The relationishp of *G. gossypioides* is therefore better established from its crossing behavior with the members of other genome groups, notably the A genome, which may be closest to the hypothetical ancestral type (Beasley 1942, p. 48).

If we consider the crossing behavior of the members of the D group with other genomes, there are two or three types of behavior. Within the yellow-flowered species, there is a factor for incompatibility superimposed upon the genetic structure of one type, the D_3 species; D_3 crosses only with B and C, and gives empty seeds with A. The second yellow-flowered type, D_2, has been crossed with C, but with neither A nor B. In contrast, the

white- or pink-flowered species, D_1, D_4, D_5 and *G. gossypioides*, have all been crossed with the ancestral type A, even though the cross is usually effected with difficulty (Skovsted 1935, 1937; Webber 1939; Beasley 1942; Stephens 1944).

Two of these species, D_4 and D_5, have been crossed with tetraploid A by Stephens (1942), who reported the crosses more easily obtained than with diploid A. *G. gossypioides* likewise crosses more easily with tetraploid A than with diploid A. *G. gossypioides* has been crossed with the synthesized amphiploid *arboreum-anomalum*, and seeds have been obtained from crosses on the synthesized amphiploids *arboreum-thurberi* and *arboreum-stocksii*. Crosses of D_1 on doubled *arboreum-thurberi* fall at one month; those of D_5 usually fall, but several seeds have been obtained, and four possible hybrids. The difference in crossing behavior toward tetraploids, in particular tetraploid A, constitutes a distinct difference between *G. gossypioides* and *G. thurberi*, and establishes a point of similarity between *G. gossypioides* and *G. raimondii* and *G. aridum*.

All of the D species have been crossed with *G. hirsutum*. Each produces a vigorous hybrid with the exception of D_3 and *G. gossypioides*. The hybrid of *G. hirsutum* × *G. aridum* suggests a low degree of incompatibility in that although vegetative growth is vigorous, the flower is abnormal, being characterized by extrusion of the style and stigma above a reduced corolla. This peculiarity has been reported also by Skovsted (1935) for the same hybrid. Flowers of *G. aridum*, the D_4 species, have not been available for crossing attempts with *G. gossypioides*. Like *G. raimondii*, and unlike *G. thurberi*, *G. gossypioides* crosses readily with tetraploid species and hybrids. Although the D_2 species also cross readily with tetraploids, they are separated from *G. gossypioides* in other respects, in particular their ease in crossing with hexaploids (Brown and Menzel 1950). *G. raimondii* crosses readily only with the hexaploid involving E; it can be crossed with difficulty with the hexaploid of A. D_1 likewise crosses with difficulty with the A hexaploid, the only hexaploid with which it has been crossed. *G. gossypioides* has not been crossed successfully with any hexaploid, but bolls containing abortive seeds sometimes remain on the A hexaploid until maturity, and a hybrid may eventually be obtained from this cross. Conclusions based on present experimental and morphological data point to a closer relationship of *G. gossypioides* to *G. raimondii* than to any other American wild species. Because no viable hybrids have thus far been obtained between *G. gossypioides* and other species of the D genome, and because of the somatic incompatibility of its hybrids with species of other genomes, *G. gossypioides* should be placed in a genome category of its own, D_6.

The incompatibility of G. gossypioides. Despite the cytological differen-

tiation between the genomes A, B, C, D and E, members of each genome in *Gossypium* can be crossed with species in one or more other genomes. Conversely, species within a genome with little or no cytological differentiation may fail to cross. Each species shows a range of crossability with other species. Even though each species can be crossed with one or more other species, there is no diploid species which does not exhibit failure to cross with some species.

There are several levels at which hybridization between two *Gossypium* species may fail: (1) Flowers drop soon after pollination without perceptible enlargement of the ovary; this is in contrast to the behavior of the ovary of *G. hirsutum* following emasculation without pollination, in which case the ovary enlarges several days before an abscission layer is formed. (2) The ovary enlarges, and the young boll remains on the plant several days to several weeks; in these cases pollination and possibly fertilization have occurred. (3) Bolls mature, and contain either abortive seeds, or large empty seeds. In rare instances a hybrid embryo may mature, which may be smaller than normal. (4) Hybridization may fail after the development of an embryo; the seed germinates, and the seedling dies in the cotyledon stage. (5) Death of the seedling occurs after several leaves are formed; in some cases plants reach the flowering stage.

In most species crosses in *Gossypium*, fertilization occurs, and development of the ovules, or capsules, or both, is initiated. The determination of how and why particular crosses fail must await histological studies, but the non-parallel development of embryo, seed coat and capsule is evident from an examination of bolls from unsuccessful or difficult crosses. The physiological processes responsible for the development of different parts of the boll are interrupted at different thresholds, so that development of all parts does not cease simultaneously. Some types of seed failure, e.g. mature bolls containing well developed seed coats without embryos, suggest that once certain thresholds are crossed, the processes involved may continue more or less autonomously, regardless of the subsequent fate of the tissue which produced the initial stimulus. When viable seeds are formed, there are again several thresholds which must be crossed before a hybrid can be called successful.

Other than hybrids involving D_3 or D_6, only three combinations giving viable seeds are known which show post germination incompatibility: $A_1 \times D_4$, $B_1 \times E_1$ and $E_1 \times D_1$. Most crosses involving D_3, including crosses with other D species, give empty seed; two, $(AD) \times D_3$ and $D_{3\text{-}d} \times D_1$, die in the cotyledon stage; one cross dies at a later stage after several leaves are formed, $E_1 \times D_{3\text{-}k}$. The incompatibility of D_3 has been reported repeatedly and discussed at length (Harland and Atteck 1931; Skovsted 1937; Silow 1941; Stephens 1942, 1945; Brown 1951). The development of

mature bolls with large empty seeds, and of plants which die in the cotyledon stage, indicates that the incompatibility is zygotic.

In the case of *G. gossypioides*, it appears that the incompatibility is similar in effect, but different in degree, since a greater number of hybrid combinations survive to and beyond the cotyledon stage. From the crosses $D_6 \times D_1$, $D_6 \times D_{2\text{-}2}$ and reciprocal, $D_6 \times D_5$, and $D_{3\text{-}d} \times D_6$, plants have been obtained which die in the early cotyledon stage, without unfolding of the cotyledons, and before the hybrid constitution could be verified. The incompatibility with the A and B species is less, hybrids with *G. herbaceum*, *G. arboreum*, *tetraploid G. arboreum*, *G. anomalum*, and the synthesized amphiploid *arboreum-anomalum* living until several leaves are formed. Incompatibility with the natural amphiploid $(AD)_1$ is least, these hybrids living until flowering. This incompatbility is marked by a gradual cessation of growth, accompanied by internal necrosis of the stem, and followed by eventual death of all tissue. The late onset of the incompatibility, and the gradual course of its morbid symptoms, suggest that failure of the hybrid is due to a deficiency of some essential metabolite, or to an accumulation of a metabolic by-product.

SUMMARY

1. Despite the failure thus far to obtain viable confirmed hybrids of *G. gossypioides* with other American wild species, the pairing behavior in the F_1 hybrid of *G. hirsutum* × *G. gossypioides*, i.e., 13 small bivalents and 13 large univalents, confirms *G. gossypioides* as a member of the D genome group.

2. Because *G. gossypioides* fails to conform in crossing behavior to any other member of the D genome, including *G. thurberi*, the species is assigned a separate subscript, i.e., D_6.

3. The incompatibility of *G. gossypioides* extends, in varying degrees, to all recognized genome groups of the genus so far tested. It is therefore different from the incompatibility existing between any other two species of *Gossypium*.

4. The gradual decline of certain F_1 interspecific hybrids involving *G. gossypioides*, following apparently normal early growth, suggests that the incompatibility leads to a deficient production of some essential metabolite, or to an accumulation of a metabolic by-product.

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STUDIES ON THE MORPHOLOGY AND CYTOLOGY OF ITERSONILIA PERPLEXANS DERX

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The organism which was used at the beginning of this investigation was isolated in April, 1947, at Baton Rouge, Louisiana, from a pustule of the rust *Kunkelia nitens* on dewberry. It was obtained, quite by accident, by Dr. S. J. P. Chilton, who was making germination studies on the teliospores of the rust. Pieces of dewberry leaves containing telial sori were inverted over tryptose agar and the spores allowed to fall onto the surface of the agar. Spores of the fungus used in this investigation were found germinating among the rust spores and producing branched, septate hyphae with clamp connections. Since the organism appeared to be somewhat unusual, the writer isolated it for further observation. During the course of these studies, Derx (1948) published an article in which he described the fungus under a new genus of the Sporobolomycetaceae as *Itersonilia perplexans*. Derx had also isolated it from the telial sori of a rust; namely, *Puccinia malvacearum* on *Althea rosea*. In spite of a few differences in micro-dimensions, there can be little doubt that the Louisiana collection and the fungus described by Derx are the same species.

As Derx pointed out, *Itersonilia perplexans* had undoubtedly been observed and even illustrated earlier by Stempell (1935), who thought that it represented a stage, which he called "Myzel II," in the development of *Entyloma calendulae* in culture. It is fairly certain that Stempell's Entyloma material was contaminated with *I. perplexans*.

Nyland (1949) has recently described a new species of *Itersonilia* which he named *I. pyriformis*. It is obviously closely related to *I. perplexans* if not a variant of it. The chief difference between the two appears to be in the presence of a clamp connection at the base of the sporogenous cell ("chlamydospore") of *I. perplexans* and its absence in *I. pyriformis*.

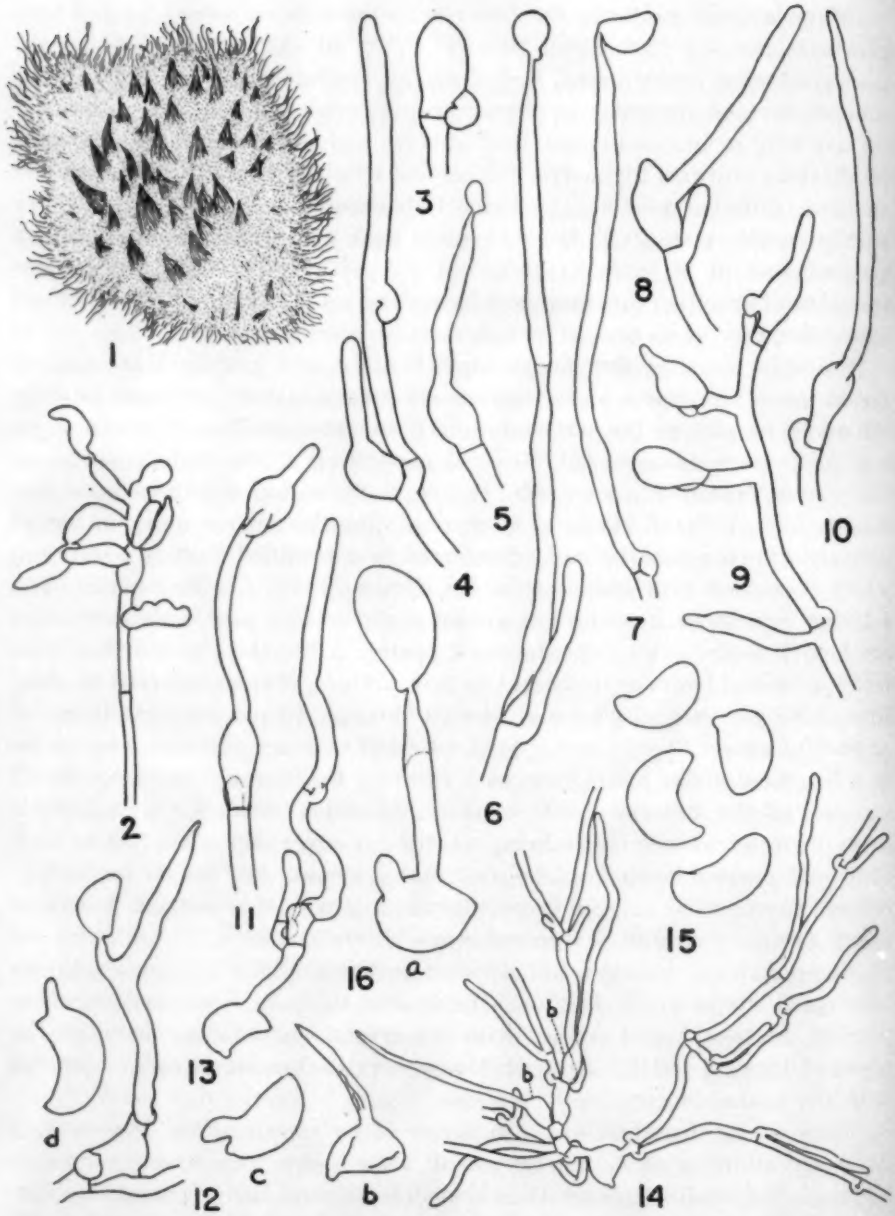
While the present investigation was in progress, the original culture isolated in Louisiana was lost, apparently as a result of unfavorably high temperatures that prevailed in the laboratory during the summer months. Fortunately, however, the writer was able to conclude this work with the use of a culture sent to him by Dr. Victor Cutter of Yale University. This culture appears to be identical with the collection obtained in Louisiana. Dr. Cutter reports that the organism was found on several occasions growing in necrotic areas on parsnips. It is not known whether *I. perplexans* may exist as a primary pathogen, but it is strongly suspected that it may occur as a secondary invader in a number of diseases.

Materials and methods. For best results the cultures were grown at temperatures ranging from about 20°–25° C. At 30°–32° C. some abnormalities in mycelial development, including the production of abnormal clamp connections and irregular hyphae, were observed. The organism does not survive long in cultures maintained at these higher temperatures. The most satisfactory cultures for morphological and cytological study were obtained on three different media: (1) Difco Sabouraud's dextrose agar, with or without yeast extract, (2) Difco tryptose agar with 5 per cent sucrose and a small amount of yeast extract, and (3) Difco yeast-beef-extract agar. On oatmeal agar there was no sporulation and mycelial growth was confined almost entirely to an area at or below the surface of the agar.

Suitable material for morphological study was prepared by making direct mounts in water or in carmine staining solution. Attempts to stain the nuclei by placing the material directly in either carmine or orcein staining fluids were unsuccessful. Nor did pre-killing of the material enhance the results. However, a successful technique for staining with carmine was finally devised. Small blocks of agar containing the fungus were cut out of actively growing colonies and transferred to a modified Carnoy's solution, which was used with good results by Hirsch (1949) on *Hypomyces*. The solution consists of a mixture of glacial acetic acid (1 part), absolute ethyl alcohol (2 parts), and chloroform (3 parts). After the material has been left for several hours or overnight in this mixture, it is transferred to absolute or 95 per cent alcohol and carried through 10 per cent gradients of alcohol to water. From water it is transferred to 4 per cent iron alum solution for three to five hours, then back to water for thorough washing. Small amounts of the material are then placed on slides, each slide containing a drop of propiono-carmine staining solution. A cover slip is applied to each drop and pressed down until the material is spread out. Nuclei in the mycelium, sporogenous cells, and spores stain well with this method. The technique was not found to be applicable when orcein is used.

Some material was also killed either in the modified Carnoy's solution mentioned above or in formal-acetic-alcohol mixture, then embedded in paraffin, sectioned, and stained with the crystal violet-iodine technique as outlined by Sass (1940). In neither case were the results as satisfactory as with the iron-alum-carmine technique.

Some of the material was also prepared by smearing the fungus in a little egg albumen on slides. Several of these slides were fixed in formal-acetic-alcohol and others in Allen's modification of Bouin's solution. Following both treatments the slides were washed, dehydrated in the alcohols, and carried back down through the alcohols prior to staining in either crystal violet or Heidenhain's haematoxylin. Difficulty in destaining made the crystal-violet technique of little use here, but some fairly good results were



FIGS. 1–16. Morphology of *Itersonilia perplexans*. FIG. 1. Small colony 48 hours old on agar. ×30. FIG. 2. Hypha producing conidia in flooded culture. ×1080. FIG. 3. Sporogenous cell. ×700. FIG. 4. Germinating sporogenous cell with hypha proliferating from below. ×700. FIGS. 5–10 Stages in development of sporophores and ballistospores. Note absence of distinct sporogenous cell in fig. 7. ×700 except figure 9 ×450. FIG. 11.

obtained with the haematoxylin. Practically all of the illustrations of cytological developments were made with the use of material stained either with the iron-alum-carmine technique or with Heidenhain's haematoxylin. In general the clearer nuclear details were obtained with the former.

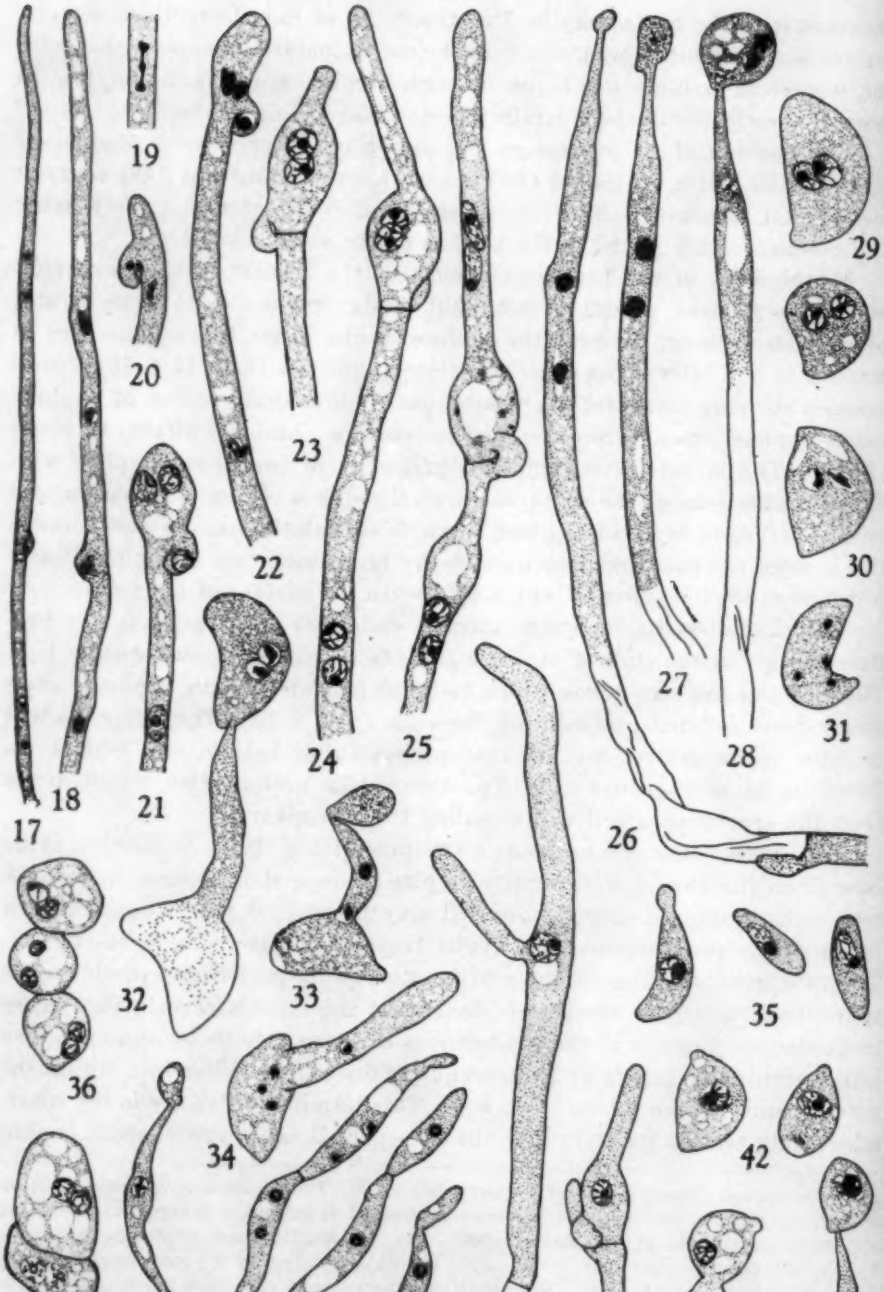
The Spencer phase microscope has also proved very useful in some of these studies. With the use of the dark contrast medium and light contrast medium oil immersion objectives it was possible to determine the number and position of the nuclei in the hyphae of the various cultures.

Morphology of the fungus. On most of the culture media used, *Itersonilia perplexans* produces somewhat fluffy colonies with considerable hyphal development beneath the surface of the agar. The colonies are at first white and later become slightly tinted with tan (figs. 44 & 45). Small colonies showing abundant sporulation and characteristic cones of agglutinated hyphae arising from the surface may be obtained within 48 hours (fig. 1). The mycelium is composed primarily of branching hyphae with clamp connections at the septa. Sections through a colony reveal an upper loosely arranged layer of hyphae in which sporulation occurs and beneath this a more compact and somewhat fleshy layer, made up of rather closely interwoven hyphae, most of which is beneath the surface of the agar.

The characteristic lunate to obovate spores of *I. perplexans* are produced singly at the ends of elongate threads which taper toward their tips. These thread-like structures, which look like long sterigmata, typically arise singly from inflated probasidium-like cells (figs. 3–10). The latter, as will be later demonstrated, are not true probasidia or basidia and will be referred to as *sporogenous cells*. The thread-like prolongation which arises from the sporogenous cell will be called the *sporophore*.

The sporogenous cell arises as a swelling with a clamp connection at its base from the end of a vegetative hypha or on a short lateral branch. A terminally produced sporogenous cell may become lateral in position as a result of the proliferation of a hypha from immediately below it (fig. 4). The sporogenous cell germinates without a resting period and produces the sporophore, which is variable in length as the figures reveal. The entire protoplasmic contents of the sporogenous cell pass into the sporophore. The latter eventually tapers at its tip and produces a swelling into which the protoplasmic contents pass (figs. 5–7). This terminal structure is the spore, adequately termed by Derx the "ballistospore," *i.e.*, a spore which is shot

Sporogenous cell formed at end of a sporophore. × 700. FIG. 12. Sporogenous cell with bifurcate sporophore. Ballistospore has been discharged from longer prong, and remaining structures are devoid of cytoplasm. × 450. FIG. 13. Ballistospore producing a septate hypha with clamp connections. × 450. FIG. 14. Major portion of a young mycelium produced by a single ballistospore. Note that two sporogenous cells have already been produced (b, b′) one of which (b) has discharged a ballistospore. × 300. FIG. 15. Ballistospores. × 700. FIG. 16, a–d. Ballistospores germinating by repetition. × 700.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away from the sporophore. The ballistospore resembles a large basidiospore and like a typical basidiospore is shot away at maturity. But the term basidiospore is inadequate here, since the spore is not produced by a true basidium.

Occasionally a sporogenous cell, instead of giving rise to a sporophore, produces a hypha at the end of which a second sporogenous cell is produced (fig. 11). In a number of cases, the ballistospore arises from a sporophore which has no inflated sporogenous cell at its base (fig. 7). It appears that, in such cases, a terminal unmodified hyphal cell may become a sporophore directly without the intervention of an enlarged sporogenous cell. Rarely the sporophore becomes forked apically (fig. 12). Whether such a sporophore is ever capable of producing two viable ballistospores has not been determined. The one illustrated had shot off a single ballistospore and the remaining spore, devoid of protoplasm, developed no further.

The ballistospores, which are typically somewhat curved and apiculate (fig. 15), may germinate by repetition (fig. 16, a–d) or by means of germ tubes (fig. 13). Those of the Louisiana collection measured 7.6–10.6 × 12.2–18 μ. A number of single-spore cultures were obtained, and these were found to develop into colonies similar to those described above. Each ballistospore produced one or more germ tubes which branched and became septate, with clamp connections appearing at all the septa (figs. 13 and 14). Within about 24 hours some of the mycelia from single spores, although still quite limited in extent, were producing sporogenous cells and ballistospores (fig. 14).

In addition to structures thus far described, certain chlamydospore-like cells produced singly or in short chains were found in cultures several days old. These cells, which will hereafter be referred to as chlamydospores, are formed most abundantly just above as well as below the surface of the agar

FIGS. 17–43. Cytology of *Itersonilia perplexans* (All figures × 1300, except fig. 17, × 550.) FIGS. 17 & 18. Terminal portions of hyphae, showing clamp connections and binucleate cells. FIG. 19. Nuclear division in a hypha. FIG. 20. Conjugate nuclear division and clamp formation in a hyphal tip. FIGS. 21 & 22. Formation of sporogenous cells. FIGS. 23–28. Stages in germination of sporogenous cells and production of ballistospores. FIG. 29. Binucleate ballistospores. FIGS. 30 & 31. Conjugate nuclear division in the ballistospores prior to germination. FIGS. 32 & 33. Germination of the ballistospores by repetition. FIG. 34. Quadrinucleate ballistospore producing a germ tube. FIG. 35. Uninucleate conidia from a flooded culture. FIGS. 36 & 37. Binucleate chlamydospores. FIG. 38. Conidium from conidial culture producing a ballistospore. FIG. 39. Budding conidia from a conidial culture. Note that a mitotic division of the nucleus has occurred in two of the conidia. FIG. 40. Uninucleate hypha produced by a conidial culture on yeast-beef-extract agar. FIG. 41. Uninucleate sporogenous cell with false clamp produced by conidial culture on yeast-beef-extract agar. FIG. 42. Uninucleate ballistospores produced by cultures derived from single conidia. FIG. 43. Germination of the uninucleate ballistospores, one by germ tube and the other by repetition. (Figures 17–19, 22, 26–28, 30–34 from material stained with Heidenhain's haematoxylin; 20, 36, 37, with crystal violet; the remainder with iron alum propionocarmine.)

in the more compact portion of the colony. They become filled with oil droplets and upon aging develop walls slightly thicker than the walls of the hyphae. Their function has not been determined, but it is considered likely that under appropriate conditions they may germinate vegetatively.

Until recently no other spore forms had been observed in this fungus by the writer. Dr. Cutter, however, pointed out that he had been able to obtain conidia by flooding with water cultures grown on yeast-beef-extract agar. The experiment was repeated by the writer and large numbers of conidia were obtained. Of several agars used, only the yeast-beef-extract agar was found to be satisfactory. Very few conidia were produced in flooded cultures grown on the other media. It was found that flooding of cultures brings about the production of numerous slender hyphae by the fungus colonies, and the conidia are budded out near the ends of these hyphae (fig. 2). The conidium-producing hyphae are septate and without clamp connections, and the cells from which the conidia arise are usually somewhat enlarged. The conidia are usually more or less curved and tapered towards each end.

Some of the water containing numerous conidia in suspension was drawn off from the flooded cultures and plated out on fresh yeast-beef-extract agar. The conidia continued to bud and formed numerous small, white, yeast-like colonies. These colonies generally develop concentric ridges as they enlarge (fig. 46). A microscopic examination of such a colony reveals the presence of budding conidia similar to those produced by the flooded cultures, as well as some short hyphal elements (fig. 47). The conidia are capable of budding at both ends to form new conidia, and chains of varying lengths are formed. Some of the hyphal elements protrude above the surface of the conidial colony and produce ballistospores either directly or through the intervention of sporogenous cells. The same hyphal element that produces a ballistospore may also bud out conidia (fig. 48). It was also discovered that some of the conidia were able to produce ballistospores, which probably accounts for the abundance of small ballistospores in some of the cultures.

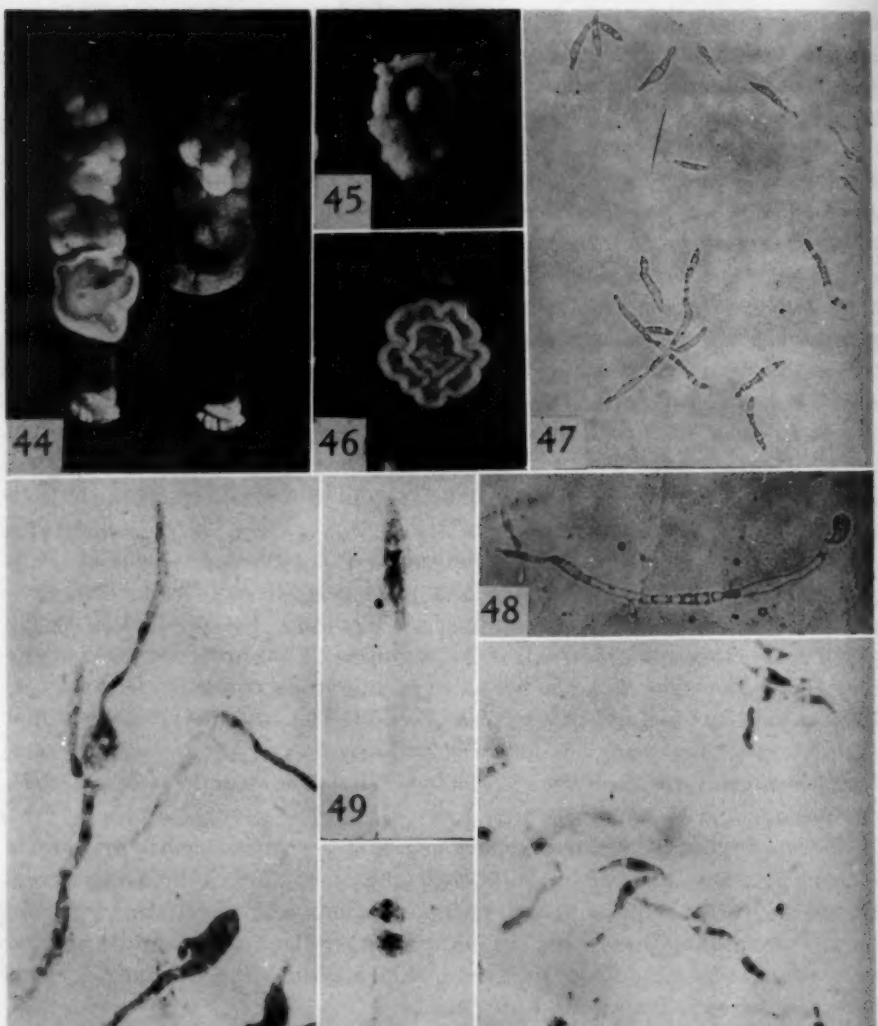
Aqueous dilutions of eight conidial cultures were made and these were plated out on agar. Single conidia were then isolated and placed on yeast-beef-extract agar. With the exception of one culture, the conidia gave rise to yeast-like colonies similar to those already described. In the exceptional culture, the conidia either failed to germinate or else they produced a few irregular hyphae which soon aborted. As long as conidial cultures are propagated on yeast-beef-extract agar, they will generally continue to remain yeast-like. Some hyphae are produced, but the conidial type of development predominates. If a conidial culture is transferred to Sabouraud's agar, however, mycelial development is favored and a fluffy colony is produced. If a portion of this colony is transferred back to yeast-beef-extract agar, it

remains mycelial and produces no conidia. In any case, the mycelium is composed of hyphae which at first sight look very much like those previously described as being typical of the fungus. However, a closer examination brings out the fact that the clamp connections are incomplete; *i.e.*, the clamp tips do not fuse with the hyphae. Furthermore, a protrusion very frequently develops on the hypha where the clamp tip touches it, and this protrusion develops into a hyphal branch (fig. 41). Also the clamp tip itself may coil around and grow out into an irregular branch. These mycelia with false clamps produce ballistospores in large numbers, either from unmodified hyphal cells, or more often from sporophores that arise from inflated sporogenous cells. The ballistospores, like those described for typical cultures of the fungus, germinate by repetition or by means of germ tubes. They have never been observed producing conidia under any circumstances. Chlamydospores are also produced singly or in short chains in older cultures. Recently attempts have been made to "cross" cultures derived from single conidia to see if mycelia with true clamps could be obtained. These experiments have not yet proved successful.

Cytological investigations. In cultures of *I. perplexans* isolated from nature, the cells of the hyphae are long and binucleate, and true clamp connections are present at all the septa (figs. 17 & 18). The production of the clamp connection and cross wall is accompanied by the customary conjugate nuclear division (fig. 20). Occasionally an apparently independent nuclear division may be observed in a hypha (fig. 19). The spindles are quite small and a chromosome count has not been possible. In the metabolic stage each nucleus contains a conspicuous nucleolus, chromatin strands, and a nuclear membrane (figs. 24 & 25).

The formation of the sporogenous cell is also accompanied by conjugate nuclear divisions and clamp formation (figs. 21, 22 & 49). A septum is formed at the base of the binucleate sporogenous cell, while the tip of the uninucleate clamp fuses with the uninucleate cell on the opposite side of the septum. The nucleus in the clamp migrates into the hyphal cell, thus restoring the binucleate condition (fig. 24).

Before the carmine staining technique was used, it was believed that nuclear fusion occurred in the sporogenous cells. Generally these cells become overstained when haematoxylin is used, thus making accurate observations on nuclear behavior difficult. Nyland (1949) reports the same difficulty with haematoxylin in his study of *I. pyriformis*. He believed that nuclear fusion occurred in the sporogenous cells ("chlamydospores") of that species. The writer is unable to demonstrate a nuclear fusion in the sporogenous cells of *I. perplexans*. On the contrary, as the sporogenous cell germinates, the cytoplasm of the cell and the two nuclei pass up into the sporophore and from there into the single ballistospore formed at the tip of



FIGS. 44–52. Photographs of *Itersonilia perplexans*. FIG. 44. Test tube cultures; single-ballistospore culture at left, culture from mass transfer at right. Nat. size. FIG. 45. Colony on agar plate. × 1.5. FIG. 46. Conidial culture on yeast-beef-extract agar. × 3. FIG. 47. Budding conidia from a conidial culture. × 185. FIG. 48. Hyphal element from conidial culture producing a ballistospore and budding out conidia. × 185. FIG. 49. Bi-

the sporophore (figs. 23–28). The ballistospore is discharged in the binucleate condition (figs. 29 & 51). Later, conjugate divisions may be observed in the ballistospore during or prior to the formation of one or more germ tubes (figs. 30, 31 & 34). On the other hand, germ tubes may be produced before nuclear divisions occur in the spore. When germinating by repetition each spore produces a sterigma-like projection of variable length at the tip of which is produced a new ballistospore. The two nuclei and cytoplasm pass from the old spore into the new one and the latter is shot away (figs. 32 & 33).

Chlamydospores produced by dikaryotic mycelia are binucleate (figs. 36 & 37). The best staining of these structures was obtained with crystal violet. The older chlamydospores have slightly thickened walls that frequently stain purple. In older cultures many of these undergo cytoplasmic and nuclear degeneration and their walls often collapse. In all stages of development they appear to be binucleate. The term *chlamydospore* as applied here designates a vegetative cell and is not to be confused with the inappropriate usage of the term in reference to brand spores of smut fungi in which nuclear fusion occurs. The chlamydospores range from globose to clavate and are often irregular in shape.

Conidia produced in flooded cultures are uninucleate (fig. 35). Conidial colonies grown on yeast-beef-extract agar are composed of similar uninucleate conidia which may bud at either end (figs. 39 & 52). During the process of budding, nuclear division occurs in the conidium, and just after this division a vacuole appears between the two daughter nuclei as they move apart (fig. 39). Occasionally a conidium produces a uninucleate ballistospore (fig. 38). The short hyphal outgrowths which frequently appear in conidial colonies on yeast-beef-extract agar are uninucleate (fig. 40). They are usually limited in development. Some of these hyphae act as sporophores and produce uninucleate ballistospores, or ballistospores may be produced by sporogenous cells which sometimes appear on these hyphae (fig. 41).

As has been previously mentioned, when conidial cultures are transferred to Sabouraud's agar they become mycelial. The hyphae are composed predominantly of long uninucleate cells with incomplete clamps. The clamps may or may not contain a single nucleus. Occasionally two nuclei may be found in a cell, but this condition is probably brought about by a mitotic

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nucleate hyphal tip with uninucleate clamp, probably a young sporogenous cell, ×780. FIG. 50. Sporogenous cells, one producing a binucleate sporophore. ×780. FIG. 51. Ballistospores, the upper spore showing the binucleate condition. ×490. FIG. 52. Budding conidia stained with carmine to show uninucleate condition. ×600. (Figures 49–51 are stained with Heidenhain's haematoxylin.)

division of the nucleus prior to cell division or the formation of a lateral branch.

It was found that the nuclear condition of the hyphae could be readily determined in living material with the phase microscope. The nucleolus, which is quite conspicuous, generally appears surrounded by a clear nuclear vacuole. The chromatin is usually not observed unless the nucleus is undergoing division. One such nuclear division was watched under the phase microscope by the writer. A relatively large nucleolus was observed beside a small spindle in a clear nuclear vacuole. In the cytoplasm slender rod-like bodies of varying length, probably mitochondria, lined up in several rows more or less parallel to the hypha near each end of the nuclear vacuole. Some appeared to be in contact with the nuclear membrane. As the division proceeded, the chromosomes, which could not be distinguished individually, appeared as a band of denser material across the equator of the spindle (metaphase). There appeared to be a centrosome at each spindle pole. The band of chromatin separated into two equal parts, which moved towards opposite poles of the spindle. At this stage (anaphase), the most rapid decrease in size of the nucleolus was observed. Also the rod-like bodies in the cytoplasm broke up into small droplets at this time. The two chromatin masses then began to round up, at which time the nucleolus was no longer visible. Later developments were not clear, as the nuclei became vague and the material was probably beginning to deteriorate by this time. The portion of the division described above occurred over a period of about 45 minutes.

Colonies on Sabouraud's agar which were derived from single conidia produce abundant sporogenous cells. The cells are uninucleate and give rise to uninucleate ballistospores (fig. 42). A few binucleate ballistospores may also be found. It seems likely that the two nuclei in these spores may have resulted from a mitotic division of a single nucleus either before or after the ballistospore was formed. The uninucleate ballistospores also germinate by means of germ tubes or by repetition (fig. 43).

Discussion. It appears that *Itersonilia perplexans* exists in nature primarily as a miktohaplont. The two nuclei in each cell are probably genetically unlike. This hypothesis is supported by the fact that single-conidial cultures do not give rise to the dikaryophase, but produce monokaryon mycelia with incomplete clamp connections. However, one would expect to be able to pair certain single-conidial cultures and obtain the dikaryotic mycelium. Although this has not yet been accomplished, experiments along this line are being continued.

Nyland (1949) reported that the ballistospores of *I. pyriformis* are binucleate and that they give rise to binucleate mycelia. He further stated that "as far as could be determined, the chlamydospores [sporogenous cells]

at maturity are uninucleate, probably containing a diploid fusion nucleus." Since Nyland mentions that he experienced considerable difficulty in obtaining good stained preparations, there is still some doubt as to whether karyogamy occurs in that species. It is hoped that future cytological studies will clarify this point.

The relationships of the Sporobolomycetaceae to other groups of basidiomycetes are not clear. Until recently the family contained the two genera *Sporobolomyces* and *Bullera*, both of which typically produce yeast-like colonies comprised of cells which reproduce either by budding or by the production of ballistospores. The investigations of Buller (1933) have shown that the cells are uninucleate and that the ballistospores are discharged by the droplet mechanism which he described earlier. Buller, as well as Kluyver and van Neal (1924), believed that these fungi were reduced basidiomycetes. Some investigators have placed them among the yeasts. Derx (1930, 1948) has stated that he believes these fungi should be included in the basidiomycetes, but he has little to say concerning their taxonomic position in that class. The prominent feature of germination of the ballistospores by repetition would seem to indicate that the group should be placed, at least tentatively, in the heterobasidiomycetes.

Derx (1948) has recently amended the description of the Sporobolomycetaceae to include *Tilletiopsis* and *Itersonilia*. These two genera are both characterized by abundant mycelial development and the production of ballistospores. Little is known concerning the development of *Tilletiopsis*. The presence of a dikaryotic mycelium with clamp connections in *Itersonilia* might raise a question as to whether such a genus could be logically included in the sporobolomycetes. On the other hand, Derx has reported that *Sporobolomyces* cultures may spontaneously give rise to a mycelial (or pseudomycelial) form which produces sterigmata on which ballistospores arise. Apparently no clamp connections are produced. Such a form, however, would certainly resemble more closely the monokaryon mycelial cultures of *I. perplexans* than the typical dikaryon cultures of that fungus. Also the yeast-like cultures of *I. perplexans* show some degree of similarity to the typical yeast-like growth of *Sporobolomyces*. It is therefore believed that until more is known about this group of organisms *Itersonilia* should be retained in the Sporobolomycetaceae.

At this time it would be useless to speculate extensively on the possible phylogenetic origin of such a fungus as *Itersonilia*. However, the possibility that it originated from a tremellaceous ancestor should be considered. The sporogenous cell, in its form and mode of origin, resembles the probasidium of the Tremellaceae. The sporophore also resembles the elongate sterigma characteristic of some members of that family. The ballistospore resembles a large basidiospore and readily germinates by repetition, the latter charac-

teristic being a very common feature of the Tremellaceae and other heterobasidiomycetes.

SUMMARY

1. Cultures of *Itersonilia perplexans* isolated from nature are composed of dikaryotic hyphae with clamp connections. Numerous binucleate sporogenous cells with clamp connections are produced on the aerial hyphae.

2. Each sporogenous cell produces an elongate sporophore which transfers the cytoplasm and two nuclei to the single ballistospore that is produced at its tip. The spore is discharged in the binucleate condition.

3. Binucleate chlamydospores are produced singly or in chains.

4. Karyogamy has not been observed at any point in the life cycle of the organism. Single-ballistospore cultures give rise to typical colonies with binucleate cells and clamp connections.

5. Cultures on yeast-beef-extract agar, when flooded with water, produce abundant uninucleate conidia. Single-conidial cultures grown on yeast-beef-extract agar are yeast-like and consist primarily of uninucleate, budding conidia. On Sabouraud's agar these cultures become mycelial, and the hyphae are composed of uninucleate cells with incomplete clamp connections. The sporogenous cells and ballistospores are also uninucleate.

6. Attempts to "cross" conidial cultures have not yet been successful. The fungus appears to exist in nature primarily as a miktophaplont.

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MEIOSIS IN ALLOMYCES

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Previous works on nuclear behavior and meiosis in the Phycomycetes have produced no clearly definitive step by step study of the meiotic chromosomes. Investigators in the past have encountered the difficulties of producing quantities of material at meiosis, of fixing and staining, of germinating resistant structures, and, in general, of dealing with material that was hard to handle. Since they were able to find some nuclei which, with a fair amount of justification, could be called meiotic, it was possible to determine the nuclear behavior in some of the genera of the Phycomycetes. For the most part, however, cytological studies in the Phycomycetes concerned with the alternation of haploid and diploid phases have been confined to fusion nuclei, nuclear size, nuclear disintegration, and occasional meiotic figures. Reports of meiosis have been based upon these phenomena rather than upon actual study of chromosome reduction. Burgeff (1915) and Cutter (1942a and b) discovered some stages of meiosis in the Mucorales, but these stages were at random and no clear picture of meiosis and of the chromosomes was possible, although some of the figures permitted chromosome counts.

In the aquatic Phycomycetes, Edson (1915) and Kusano (1912) found nuclear divisions which were probably meiotic in *Pythium* and *Olpidium* respectively. Claussen (1908) found some evidence of meiosis in *Saprolegnia*, as did Laibach (1927) in *Monoblepharis*, and Blackwell (1943) in *Phytophthora*. While these investigators of the cytology of the aquatic Phycomycetes have found apparent meiotic nuclei and thereby established with some degree of certainty the place of chromosome reduction, none of them because of the lack of material or the smallness of the nuclei has been able to observe the various stages of meiosis or to study the chromosome number and morphology, which would be great aids in cytotaxonomy and genetics.

Since Kniep (1929, 1930) first described sexuality and an alternation of isomorphic generations in the water mold *Allomyces*, there has been a controversy as to where meiosis occurs in the two species now included in

[1] The research for this paper was carried out in part while a student at Harvard University and in part while a National Research Council Fellow at the University of California at Berkeley. I am deeply grateful to Dr. William H. Weston under whom I had the privilege of doing the research for my doctorate. I am much indebted to Dr. Ralph Emerson for his interest and help which have made this work possible and for his supplying all of the cultures used. Sincere appreciation is also felt for the generous contributions of Dr. Barbara McClintock and Dr. L. R. Cleveland.

the subgenus *Euallomyces*. Detailed discussions of this controversy have been published by Emerson (1941), Sparrow (1943), Emerson and Wilson (1949), and Emerson (1950) and will not be included here. It need only be noted that before the present study was made the place of meiosis in the life cycle of *Euallomyces* was indicated by the evidence that Kniep (1930) and Sörgel (1936) found in their studies of nuclear volume and that Emerson (1941) found in his genetic work. While these notable works had marked the approximate position of meiosis in *Euallomyces*, nothing at all was known about chromosome behavior in the very different life cycles of the other two subgenera of *Allomyces*, *Cystogenes* and *Brachyallomyces*.

Location of the meiotic divisions in the resistant sporangia of *Euallomyces* and *Cystogenes* by direct cytological observation was first reported by Emerson and Wilson (1949) who emphasized at that time the broad significance of this discovery. The present paper presents a detailed analysis of chromosome behavior in the three subgenera of *Allomyces*, reviews the three different life cycles in the light of these findings, correlates the processes of maturation and germination of resistant sporangia with meiotic phenomena, and sets forth a number of other cytological observations that point the way to basic cytogenetic and cytotaxonomic studies on *Allomyces*.

Material and methods. The species used in this study are:

Subgenus *Euallomyces*

Allomyces arbuscula var. *minor* (Ceylon 1)

A. javanicus var. *macrogynus* (Burma 1Da)

A. javanicus var. *javanicus* (Java 1)

Subgenus *Cystogenes*

Allomyces cystogenus (Burma 1B)

Subgenus *Brachyallomyces*

Allomyces anomalus (Mexico 16 and India B2)

The strains used are from among those listed by Emerson (1941) and designated above in parentheses following the specific name.

Cultures were ordinarily grown at room temperature in 20×150 mm. test tubes containing about 12 cc. of yeast-starch medium (Emerson 1941). While still hot, tubes of medium were slanted and the agar allowed to solidify. Tight cotton plugs were used to reduce evaporation, and inoculations were made near the top of the slant and allowed to grow down the tube. When the resistant sporangia were mature, they were scraped from the agar slant with a flattened wire and placed in small dishes of water and allowed to germinate. Large numbers of resistant sporangia were readily removed from the dishes of water with small pipettes and placed upon slides. As much surplus water as possible was then quickly drawn off with the pipette; a drop or two of aceto-orcein was added, and a No. 0 cover

glass placed over the stain-fixative. Excess aceto-orcein was blotted off between absorbent paper. Then, under a dissecting microscope, the cover glass was pressed with a needle to burst the sporangia. The contents of the sporangia could be pressed out in a fairly viscous mass which became fixed and the chromosomes stained. A second blotting was sometimes necessary after the pressure had been applied. The slide was then warmed over an alcohol flame. Often it was helpful to ring the cover glass with petrolatum to prevent rapid drying.

Photomicrographs were made with a Zeiss microscope equipped throughout with apochromatic lenses. Uniform magnification of approximately 2600 × has been used in the photographs.

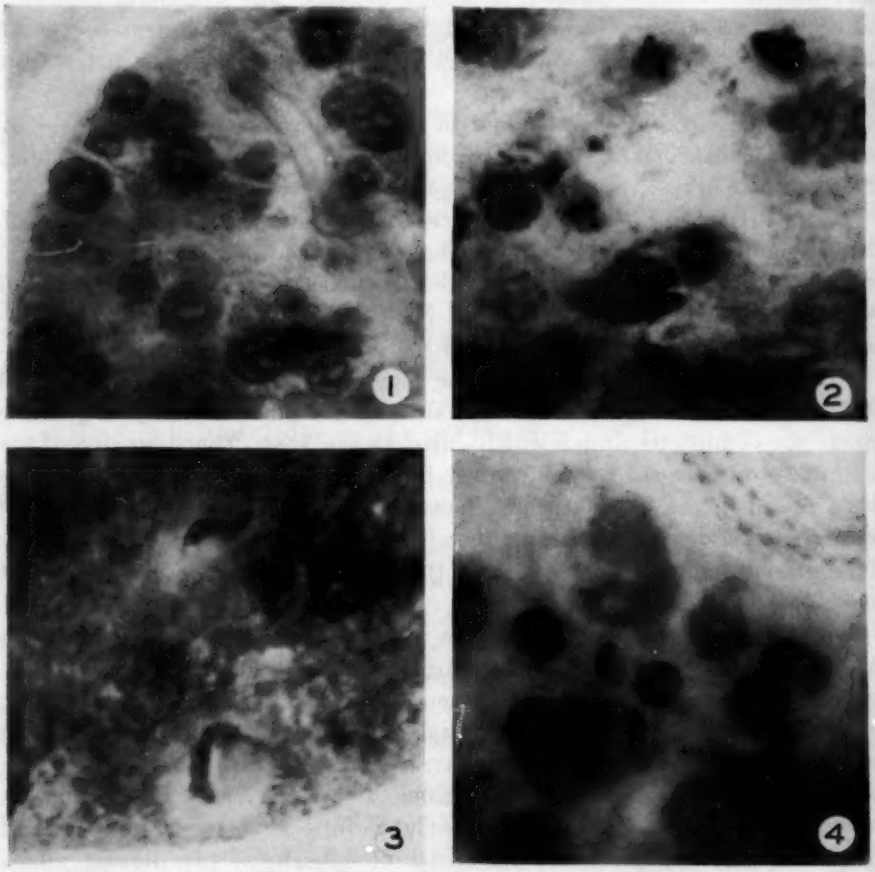
Maturation and germination of resistant sporangia. Maturation. Realizing the need of a thorough knowledge of the handling of material, Emerson and the writer jointly investigated the maturation and germination of the resistant sporangia of *Allomyces*. Not until these processes were understood could a more complete study of meiosis be made.

It had been known for some time (Kniep 1930, Hatch 1935, Emerson 1941) that resistant sporangia take definite periods to mature depending upon the conditions under which cultures are kept. The maturity of resistant sporangia can be determined by their ability to germinate. It has been found in the present study, however, that there are certain internal changes in the resistant sporangium which may be used with great accuracy for determining maturity, and that these changes must be brought about before germination is possible.

When young resistant sporangia are stained with aceto-orcein soon after being formed at the hyphal tips, the protoplasm is clear and homogeneous like that of the hyphae when stained. In 48–72 hours, however, concurrent with the thickening, pitting, and pigmentation of the sporangial wall, spherical bodies (fig. 1) appear which stain with aceto-orcein. The bodies vary in size from 1 to 4 microns. For convenience of designation these bodies have been called chromospheres in this study. Toward the end of the maturation period of the resistant sporangia, the diploid nuclei enter the prophase of Meiosis I, and the chromospheres become eroded in appearance (fig. 2) and rapidly disintegrate. A little before the complete disappearance of the chromospheres, the nuclei begin to expand and advance to the early prophase stages (fig. 2). Just after the chromospheres have disintegrated, the nuclei become arrested in the prophase of Meiosis I in the now mature resistant sporangia and remain in this stage until germination.

In order to establish more precisely the relation between chromosphere behavior and the process of maturation, the presence or absence of chromospheres in the resistant sporangia was correlated with their germinability

at intervals during a period of 80 days. For each interval of age, a sample of sporangia was taken from an agar culture of *A. javanicus* var. *macrogynus* (Burma 1Da). Half of the sample was then fixed and examined cytologically, while the other half was used to determine the percentage of germination. The results of these tests are shown in the form of a graph (fig. 5). It is apparent that the period in which the chromospheres exist is the maturation period. When the chromospheres have disappeared, the large prophase nuclei of the mature resistant sporangia (fig. 3) are left in relatively clear cytoplasm, and at this stage it is possible for germination to take place.



FIGS. 1–3. Maturation processes in resistant sporangia of *Allomyces*. Approximately × 2660. FIG. 1. Premeiotic chromospheres in the immature resistant sporangium. FIG. 2. Eroded premeiotic chromospheres and early prophase nuclei. FIG. 3. Prophase nuclei of the mature resistant sporangium after disappearance of premeiotic chromospheres. FIG. 4. Formation of postmeiotic chromospheres at resistant sporangium germination.

One can in a matter of minutes, therefore, make an aceto-orcein smear of resistant sporangia and determine their maturity cytologically rather than take an hour or so to see whether or not they will germinate. As a rule it takes 4 to 8 weeks for resistant sporangia to mature on agar cultures under conditions used in this study. Having reached maturity, if the sporangia are air dried, they will remain viable without detectable change in the nuclei up to periods of 15 years, and perhaps even longer.

Other investigators (Kniep 1930, Emerson 1941, Hatch and Jones 1944) have indicated that desiccation of the sporangia hastens the process of maturation. Even though desiccation is a positive factor in maturation, resistant sporangia will mature in water cultures (Emerson 1941), but ordinarily at a much slower rate and less uniformly than on agar cultures.

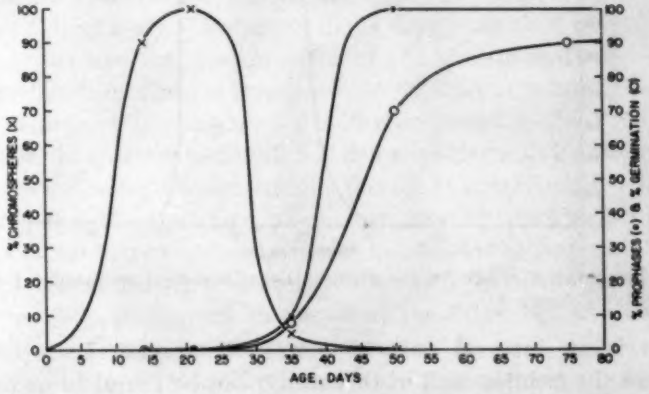


FIG. 5. Time plot of the maturation processes of resistant sporangia of *Allomyces* grown on agar.

Germination. Having established good criteria for determining maturity and having gained some insight into the optimum conditions for maturation on agar cultures, certain conditions affecting germination itself were then investigated.

It was found that temperature was an important factor for the germination of resistant sporangia. Samples of mature sporangia were germinated at various temperatures, and the percentage of germination was based upon the number that had actually discharged spores within three hours. Figure 6 shows the temperature range for germination of the resistant sporangia of *A. javanicus* var. *macrogynus* (Burma 1Da). Consequently temperatures of 20° to 25° C. were used thereafter for germinating resistant sporangia for the study of meiosis. Completely matured resistant sporangia, freshly scraped from an agar slant, of any of the strains of *Allomyces* selected for the present study will usually germinate with remarkable uniformity within this temperature range. This natural uniformity, as will be pointed out

shortly, was of great practical advantage in preparing slides to show the various stages of meiosis. With certain other isolates of *Allomyces* or with old cultures, resistant sporangia sometimes germinated in a less regular manner. It was found that a greater degree of uniformity could be artificially induced in such material by subjecting it to a low temperature during the first part of the germination period for an hour or a little longer and then placing it at room temperature for 15–20 minutes before making slides.

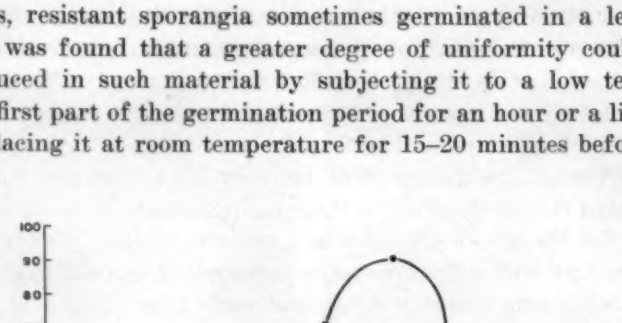


FIG. 6. Temperature range for the germination of resistant sporangia of *A. javanicus* var. *macrogynus* (Burma 1Da).

Meiosis is an integral part of germination, and the metaphases of Meiosis I, in the isolates used in this study, can be found in quantity in 55 to 65 minutes after the resistant sporangia are put into water. The metaphases of Meiosis II appear in 80 to 110 minutes, and after two hours spores begin to emerge from the sporangia. Since there are always some precocious and some straggling sporangia, the figures cited above refer to the peak waves of meiosis occurring in the germinating sporangia. By sampling, the various stages of meiosis can be timed, although the time will vary to some extent with the temperature, the strain, and the age of the culture. Germination of resistant sporangia from older, more dried cultures takes longer, and meiosis occurs much later. In sporangia dried for ten years, it takes almost a day for germination. On the other hand, in freshly matured material of some of the hybrid strains made by Emerson (1941), Metaphase I occurs as early as 35 minutes after the sporangia are placed in water, and Meiosis I is usually completed in most of the sporangia within 45 minutes.

After the second division of meiosis is completed, a substance appears in the protoplasm which stains with aceto-orcein. This substance clumps and forms small masses, and although they are not so spherical or granular, they look much like chromospheres (see above) and stain similarly (fig. 4).

These masses collect around the haploid nuclei in a cuplike fashion and become the nuclear caps, which have been described in earlier works (Barrett 1912, Kniep 1929, Hatch 1935 and 1938, Emerson 1941). In the present study they have been called post-meiotic chromospheres to distinguish them from the pre-meiotic chromospheres which are found during the maturation period. The chemical nature of the pre-meiotic and post-meiotic chromospheres is unknown, and it is not known whether they are of the same substance. The regular appearance of the chromosphere material at the formation of the motile stages, the existence of the nuclear caps throughout the motile stages, and the close association of the flagellum with the nucleus and nuclear cap suggest to the writer that the nuclear caps are related to motility rather than growth as stated by Hatch (1938). The function of the nuclear cap has long been a matter of conjecture. Barrett (1912) designated it as a "food body." Kusano (1912) suggested that the nuclear cap in *Olpidium* was like the macronucleus of the Ciliata and was concerned with food metabolism. Should this prove to be true, it would be an important point in linking the origin of the Phycomycetes to the Protozoa. The coincidence of the nuclear cap with the motile stages and its absence in the sessile stages tend to lend weight to this theory. It is noteworthy that Hatch (1935) found that the nuclear caps did not stain by the Feulgen reaction. He also concluded that these bodies were chondriosomal material, but it has usually been found that chondriosomes are easily dissolved in highly acid solutions, especially acetic acid. In this study the chromospheres and nuclear cap have withstood strong acetic acid treatment.

Allomyces is a very favorable organism for the study of meiosis and germination in that both processes can be produced at will in a very short time, and there are no seasonal factors to offer complications. That meiosis and the production of spores from a resistant sporangium are accomplished within one to two hours is advantageous for the organism. In the warm-temperate and tropical regions, in which this mold is found, cool rains may produce the stimulus for germination at a very favorable time for propagation. It is to be remembered that the first stages of meiosis have already been initiated when the resistant sporangia go into a resting condition, and, as a result, germination can proceed more rapidly. This same condition has been found in some of the Protozoa (Cleveland 1949).

Chromosome and nuclear behavior at meiosis. Meiosis in *Allomyces* follows the usual pattern found in most organisms. There are, however, some points of interest which are described below.

Prophase nuclei. When the resistant sporangia are maturing the diploid nuclei contained in the sporangia enlarge and enter the prophase of Meiosis I. These early prophase nuclei can, as explained above, be seen during the disintegration of the premeiotic chromospheres. By the time the resistant

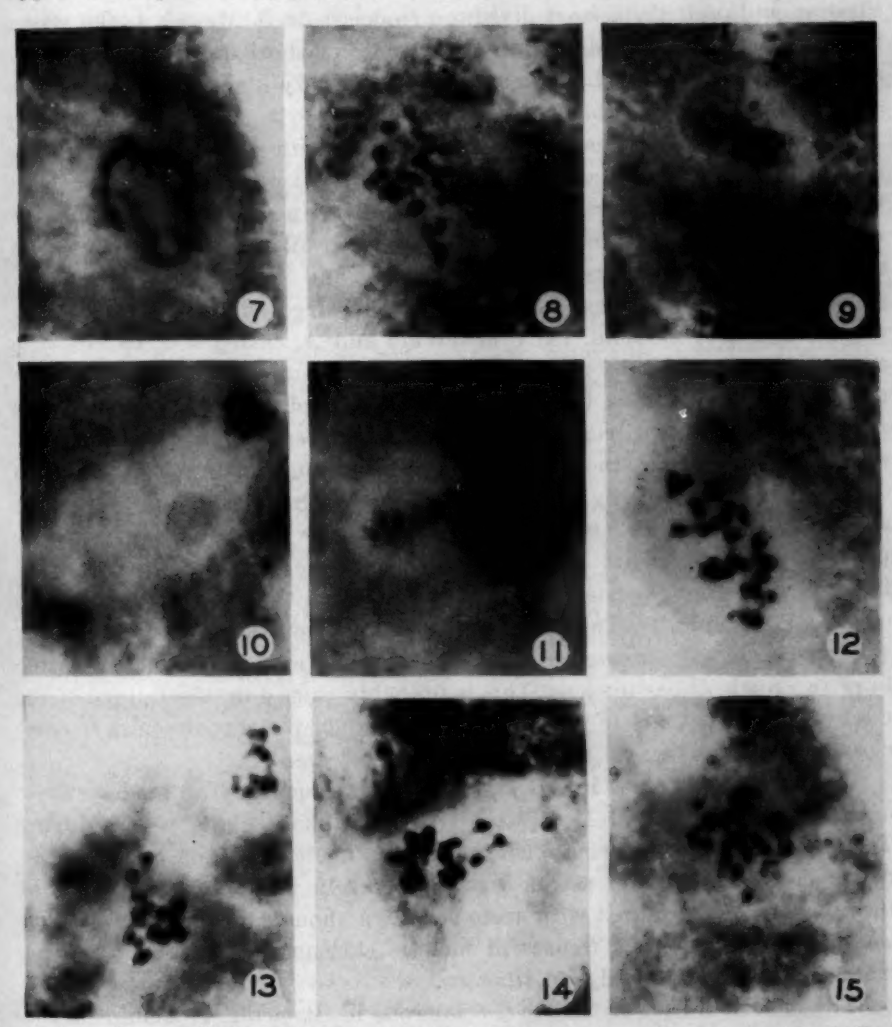
sporangia are mature, the nuclei have progressed well into the prophase of Meiosis I, and at this stage the reduction divisions are arrested until germination begins.

In the granular cytoplasm of mature resistant sporangia, the late prophase nuclei are rather discrete with a well defined nuclear membrane, large nucleolus, and partially contracted chromosomes lying in a clear nuclear sap. The nucleolus is large for the size of the nucleus. The chromosomes at this stage can be deeply stained with aceto-orcein, which is rather unusual for prophase chromosomes. In *A. javanicus* var. *macrogynus* the chromosomes in the dormant resistant sporangia form a rather loose net around the periphery of the nucleus (fig. 7), but in *A. cystogenus* the prophase chromosomes appear to clump around the nucleolus (fig. 3). In *A. arbuscula* the arrangement of the chromosomes at this stage is similar to that in *A. cystogenus,* but, even though it is hard to describe, there is enough difference by comparison so that a distinction can be made. The arrangement of the chromosomes in the prophase nuclei of the resistant sporangia varies with the species enough so that it may be used roughly for identification. The exact stage of the nuclei in the dormant sporangia is not known, nor is it known whether or not crossing-over has taken place in the chromosomes before the nuclei reach this stage. Nevertheless, the rapidity with which the nuclei in a resistant sporangium can advance to Metaphase I after being placed in water would suggest that the prophase of the mature sporangia is a late prophase and that crossing-over has already taken place.

When freshly matured resistant sporangia are placed in water, the processes of meiosis and germination are initiated at once. Within 5 to 10 minutes, the chromosomes become less dense and more granular in appearance and can no longer be stained to any great extent with aceto-orcein. The thread-like mass of chromosomes advances to a diakinesis stage (fig. 8), which can be stained with aceto-orcein if the slide is allowed to stand several hours or over night. At diakinesis the morphology of the chromosomes is more easily observed than at any other stage; the chromosomes may be seen as bivalents, and the chiasmata and constrictions may also be observed. This is also the stage in which the chromosomes are most readily counted. Further study on the morphology of the chromosomes is in prospect so that the individual chromosomes may be identified for genetic and cytotaxonomic studies.

The reduction divisions. The chromosomes continue to contract during and after diakinesis. At prometaphase they become greatly reduced in length before becoming attached to the spindle (fig. 12). The separation of chromosomes at Anaphase I (fig. 15) occurs in a very short time, and relatively few anaphase figures have been observed. The chromosomes at Telophase I (fig. 10) can be seen as distinct groups at both poles.

At no other place do the nuclei in the life cycles of *Allomyces* attain the large size that they reach in Meiosis I. After Meiosis I the nuclei become much smaller until they reach the small size of the nuclei in the vegetative hyphae. Metaphase II (fig. 11) can be found in the sporangia approximately



FIGS. 7–15. Meiotic divisions in *Allomyces*. Magnifications all approximately 2660×. Each division of scale below the figures represents 10 microns. FIG. 7. Prophase nucleus in mature resistant sporangium of *A. javanicus* var. *macrogynus* (Burma 1Da). FIG. 8. Diakinesis (Burma 1Da). FIG. 9. Side view of Metaphase I (Burma 1Da). FIG. 10. Telophase I (Burma 1Da). FIG. 11. Metaphase II, *A. javanicus* var. *javanicus* (Mexico 16). FIG. 12. Prometaphase I (Burma 1Da). FIG. 13. Prometaphase I, *A. arbuscula* (Ceylon 1). FIG. 14. Diakinesis, *A. cystogenus* (Burma 1B). FIG. 15. Anaphase I (Burma 1B).

20 minutes after Metaphase I. This indicates that the Interphase between the two reduction divisions is very short. No stages between Telophase I and Metaphase II have been observed. It is possible that the telophase chromosomes of the first division pass directly into the prometaphase of the second division and omit the second division prophase. As in Meiosis I, the stages in Meiosis II following Metaphase II are of very short duration. The cleavage of protoplasm and the formation of spores take place rapidly after the second meiotic division has been completed.

The nucleolus does not stain very deeply with aceto-orcein, but if a slide is allowed to stand several hours, the nucleoli pick up enough stain to become well defined (figs. 8, 9, 10). Except during nuclear divisions, the nucleolus is large and prominent in the nuclei at all stages in the life cycles of *Allomyces*. In *A. arbuscula*, *A. cystogenus*, and *A. javanicus* var. *macrogynus*, the nucleolar chromosome is relatively large with a long secondary constriction near one end. In *A. arbuscula* and *A. cystogenus*, by the time diakinesis is reached the nucleolus has disappeared (figs. 13, 14). In these two species at diakinesis, the bivalent of the nucleolar chromosomes with its long subterminal constrictions can usually be seen. In *A. javanicus* var. *macrogynus*, however, the nucleolus persists through Metaphase I and can often at Telophase I (fig. 10) still be seen, left near the equatorial plate after the chromosomes have gone to the poles. The large nucleolus at metaphase in this species has a tendency to distort the division figure and isolate the nucleolar chromosomes from the rest of the chromosomes at the center of the spindle. The nuclei in the hybrid of the interspecific cross (*A. arbuscula* × *A. javanicus* var. *macrogynus*) made by Emerson often have two nucleoli per nucleus. This is probably caused by the failure of the nucleolar chromosomes to pair or by the failure of the chromosomes to come close enough together so that the nucleoli coalesce.

The meiotic divisions in *Allomyces* are intra-nuclear. The nuclear membrane is still existent at Metaphase I and Anaphase I and is lost during Telophase I with the formation of daughter nuclei. Spindle fibers can be detected. Centrioles and astral rays have rarely been observed; none of these organelles is stained with aceto-orcein. Although the chromosomes are small, the characteristic figures of meiotic chromosomes caused by chiasmata are found frequently in *Allomyces*.

The meiotic nuclei are about 6–8 microns in diameter. It should, nevertheless, be remembered that such measurements are far from accurate. Varying the pressure upon the cover slip will cause the diameter of the nuclei to vary. Kniep, in his careful measurements of nuclear size in the hyphae, recognized the fact that the nuclei are ellipsoidal in shape and used two radii in calculating nuclear volumes. It is of primary importance that the nuclei do increase in size at meiosis, making the study of meiotic

nuclei less difficult. Chromosome size has not been carefully studied in this work, but it is planned, if possible, to make an idiograph of the chromosomes.

Chromosome numbers. In the present study three isolates from three species of the genus *Allomyces* were studied intensively for the determination of chromosome numbers. The isolates with their haploid chromosome numbers are as follows:

A. cystogenus (Burma 1B) 14
A. arbuscula (Ceylon 1) 16
A. javanicus var. *macrogynus* (Burma 1Da) 28

Although it is difficult to find a nucleus with all of the chromosomes in the same plane of focus, it was possible to locate and photograph a few nuclei in which most, if not all, of the chromosomes are visible. Figure 14 shows a diakinesis stage of *A. cystogenus*. Figures 13 and 12 show prometaphases in *A. arbuscula* and *A. javanicus* var. *macrogynus* respectively. In these photographs the differences in the chromosome numbers of the various species can be estimated. *A. javanicus* var. *javanicus*, so far found to have 13 to 21 chromosomes, is believed to be a natural hybrid with a variable chromosome number, and its relationship with the other species will be discussed in a subsequent paper.

While this paper was being prepared for publication, other isolates of *A. arbuscula* and *A. javanicus* var. *macrogynus* from various regions of the world were examined. It is now conclusive that polyploidy exists in these two species. Isolates of *A. arbuscula* have been found with 8, 16, 22–24, and 32 chromosomes. In a very limited investigation of isolates of *A. javanicus* var. *macrogynus*, isolates with 28 and 50 plus chromosomes have been discovered so far. These are haploid numbers. Further work is being done upon the cytotaxonomy and cytogenetics of the group and will be reported later.

Bearing of Meiosis upon the life cycles in Allomyces.

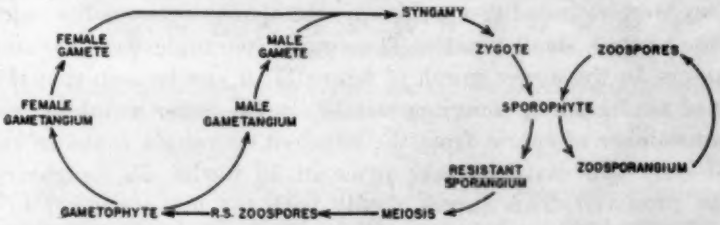


FIG. 16. Life Cycle of the subgenus *Euallomyces*.

Euallomyces. From the above observations of meiosis, it is possible to review and revise certain features of the life cycles in the genus *Allomyces*.

The subgenus *Euallomyces*, established by Emerson (1941), comprises those species in which there are both gametophytic and sporophytic plants (cf. fig. 16). As described by Kniep (1930) and Emerson (1941), the sporophytic and gametophytic phases in *Euallomyces* are equal sexual and asexual generations. The sporophytic phase of the life cycle begins at the zygote with the fusion of the two gametic nuclei and ends, as determined cytologically by the present study, at meiosis in the resistant sporangium. The nucleus of the zygote divides by mitosis to produce the nuclear population of the sporophytic plant. Upon this plant are borne two types of sporangia: one a thin-walled sporangium and the other a thick-walled resistant sporangium. Since there is no reduction of chromosomes in the nuclear divisions in the thin-walled sporangia, the nuclei remain diploid, and the uninucleate diploid spores evolving therefrom germinate to produce sporophytic plants like the parent. In the resistant sporangium, however, meiosis does take place, and the spores produced are uninucleate and haploid. Upon germination the haploid nucleus of a spore from a resistant sporangium divides mitotically to produce the nuclei of the gametophyte. The gametophytic plant bears both male and female gametangia and is self-fertile and cross-fertile. The gametophytic phase of the life cycle begins at the reduction divisions of nuclei in the resistant sporangium and ends at syngamy.

It has been found that there are no mitotic divisions of nuclei in the sporophytic resistant sporangia of *Euallomyces* after maturity. This was learned by counting the prophase nuclei before germination in a hundred mature resistant sporangia (*A. javanicus* var. *macrogynus*, Burma 1Da) selected at random, and comparing these nuclear counts with the number of spores that emerged during germination of a second random sample of resistant sporangia from the same culture. The prophase nuclei were counted in aceto-orcein smears where the entire protoplast could be clearly observed. Spore counts were made by isolating single resistant sporangia in drops of water before germination took place. Within an hour of discharge, when they were rounded and quiescent, the spores were readily counted as they flowed into a small pipette. The empty sporangia were examined for stray spores. In the upper graph of figure 17, it can be seen that the mean number of nuclei per sporangium was 13. In the lower graph of figure 17, the mean number of spores from the hundred sporangia is shown to be 56. Thus, if only two divisions take place in 13 nuclei, 52 daughter nuclei would be produced. This agrees closely with the mean number of spores produced. If there were three divisions a mean number of only 6 nuclei could be included in the sporangia to produce a mean number of 56 uninucleate spores per sporangium. Should there be only one division in the nuclei of a germinating sporangium, 28 nuclei would have to be included in the sporangia as a mean number, and no sporangium was ever found to

contain as high a number as 28. These counts of nuclei in the mature sporangia before germination and the counts of uninucleate spores emerging from the sporangia were made in collaboration with Emerson and show that only the two meiotic divisions occur in the germinating resistant sporangia of *Euallomyces* and that there are no haploid divisions in these structures

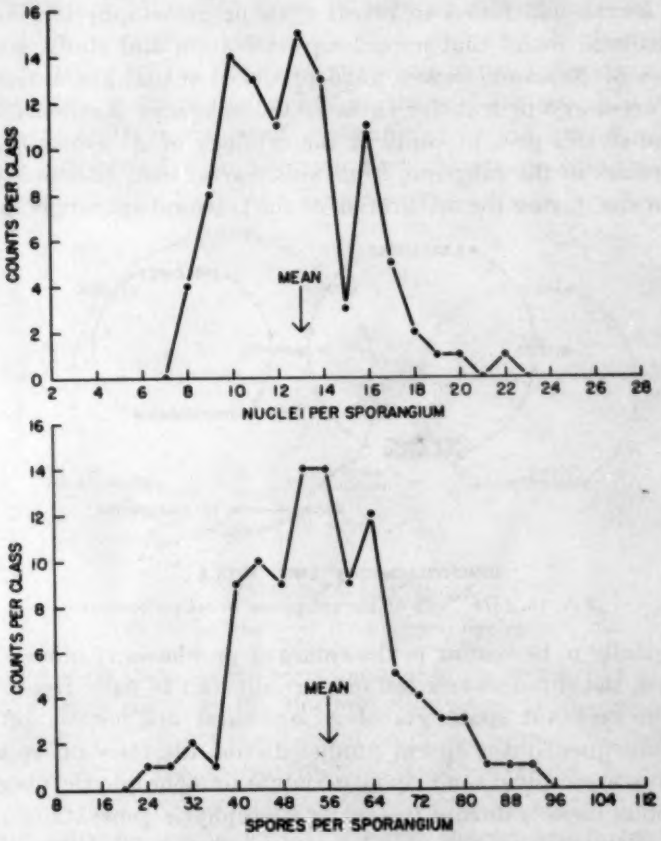


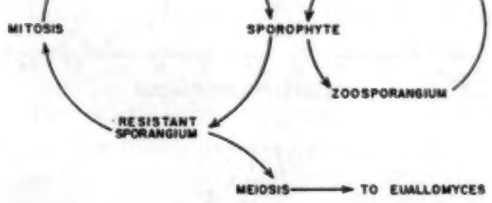
FIG. 17. Number of uninucleate spores per sporangium correlated with the number of nuclei per mature sporangium before germination in *A. javanicus* var. *macrogynus* (Burma 1Da).

after meiosis. This evidence is confirmed by cytological observation, for in all of the many germinating sporangia examined no divisions other than the two meiotic divisions have been found.

This present work proves by direct cytological evidence that the reduction of chromosome number in *Euallomyces* takes place in the resistant sporangia. It is now clear, therefore, that the life cycle of *Euallomyces*

consists of equal and alternating haploid gametophytes and diploid sporophytes.

Brachyallomyces. In 1941 Emerson established the subgenus *Brachyallomyces* and gave as its characteristic a short life cycle (fig. 18) lacking alternation of generations and sexual stage. In the discussion of *Brachyallomyces* he said that species could be placed in this subgenus only after a thorough search had failed to reveal cysts or gametophytic plants. Since then it has been found that upon long cultivation and study, some of the old isolates of *Brachyallomyces* have produced sexual generations, and it has been necessary to transfer them to the subgenus *Euallomyces*. It has been found in this present study of the cytology of *A. anomalus*, which is the sole species in the subgenus *Brachyallomyces*, that, although the nuclei increase in size during the maturation of the resistant sporangia and appear



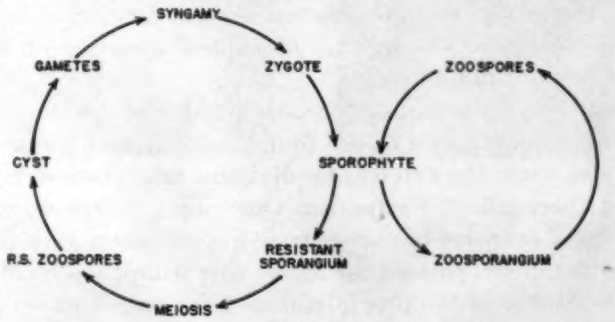
BRACHYALLOMYCES LIFE CYCLE

FIG. 18. Life Cycle of the subgenus *Brachyallomyces*.

morphologically to be similar to the enlarged prophases of other species before meiosis, the chromosomes fail or partially fail to pair. Hence the divisions in the resistant sporangia of *A. anomalus* are mitotic rather than meiotic. Consequently the spores produced from the resistant sporangia of *A. anomalus* are diploid, and upon germination sporophytic plants result. What inhibits meiosis during the many sporophytic generations of an isolate of *A. anomalus* is not known. What releases this inhibition and allows a plant to include a gametophytic phase in its life cycle is also undetermined. It is logical now, however, from what has been learned of the behavior, especially the nuclear behavior, of *A. anomalus* to consider the subgenus *Brachyallomyces* as represented by strains of *Euallomyces* in which meiosis does not occur over long intervals and in which the sexual phase is yet unknown, but in which the potentiality for reduction of chromosomes and production of a haploid generation still exists. Emerson suggested when he established this subgenus in *Allomyces* that, since species classification in *Allomyces* is based upon sexual characters, such a divi-

sion might prove to be merely a convenience until the sexual stage could be found.

Cystogenes. Emerson (1938) described in *Allomyces* a life cycle (fig. 19) in which the spores from the resistant sporangia were flagellate and formed cysts instead of germinating to produce gametophytic plants. The cyst-forming species of this type are included in the subgenus *Cystogenes*, Emerson (1941). The cysts in turn germinate and, as shown by McCranie (1942), produce isogametes. McCranie also observed that in the cleavage of spores in the resistant sporangia from one to several nuclei were included in a single spore, but he thought the spores were without flagella. Teter (1944) confirmed McCranie's observation of sexuality in *Cystogenes* but agreed with Emerson that the spores from the resistant sporangia are usually biflagellate. Teter thought it likely that the number of



CYSTOGENES LIFE CYCLE

FIG. 19. Life Cycle of the subgenus *Cystogenes*.

flagella present on these spores corresponded to the number of nuclei in the cytoplasm of each spore, and in the present study this suggestion has been proved to be correct. From the correlation of the number of flagella to the number of nuclei in the spores from resistant sporangia, Teter suggested the possibility that the first division of meiosis takes place in the resistant sporangium and the second meiotic division takes place in the cyst. This suggestion of Teter's has been found to be wrong. All of these investigators mentioned above used the same isolate of *A. cystogenus*, Emerson's Burma 1B, which was also used exclusively in the present work because of the ease with which the resistant sporangia germinate.

The nuclear behavior in *Cystogenes* was studied in the present investigation from the mature resistant sporangia on through the reduction divisions and the haploid stage until syngamy. As in *Euallomyces* reduction of chromosome number occurs in the resistant sporangia, which are borne on the sporophyte of *Cystogenes*. The sporophytic phase of the life cycle of *Cysto-*

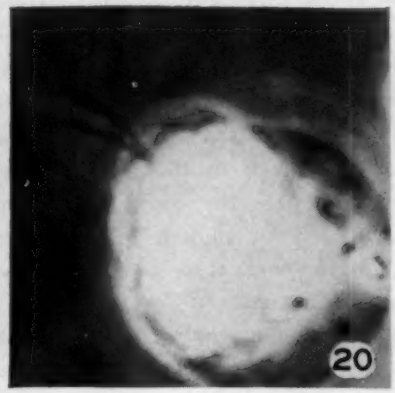
genes is similar to that of *Euallomyces* in morphology, development, and cytology. The diploid part of the life cycle begins at syngamy with the fusion of gametes, and the zygote develops into a sporophytic plant. The sporophyte of *Cystogenes* produces both thin-walled sporangia and thick-walled resistant sporangia. The thin-walled sporangia produce uninucleate diploid zoospores, which germinate to form other sporophytic plants. In the germinating resistant sporangia of *Cystogenes,* meiosis takes place in a manner much like that in *Euallomyces.* The sporophytic phase of *Cystogenes* ends at meiosis in the resistant sporangium.

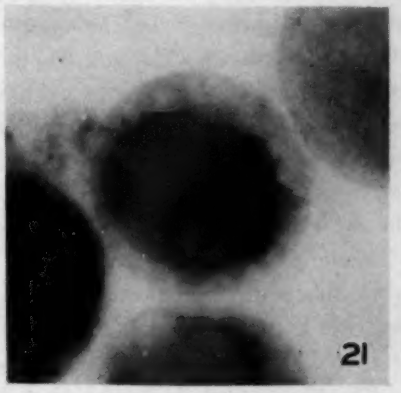
All similarity of *Cystogenes* to *Euallomyces* begins and ends with the sporophytic generation, as may be seen by comparison of the life cycle diagrams (figs. 16 and 19). The haploid phase of *Cystogenes* is greatly reduced, and the sexual and asexual generations are very unequal; in fact, as will be shown below, there is only one mitotic division of haploid nuclei in the entire life cycle. The number of haploid divisions in *Euallomyces,* on the other hand, is unlimited.

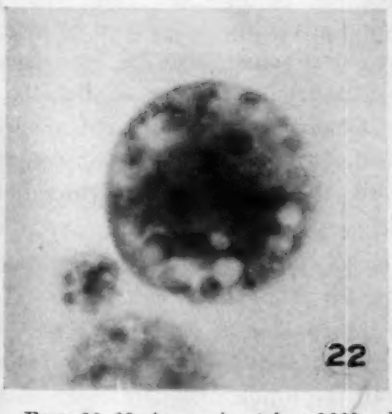
In *Cystogenes* approximately the same number of nuclei are found in a mature resistant sporangium as are found in a sporangium of similar size in *Euallomyces.* Only the two meiotic divisions take place in the germinating resistant sporangia of *Cystogenes.* One might, therefore, expect about the same number of spores to emerge from a sporangium as in *Euallomyces,* but this does not occur. Instead the nuclei pair within the resistant sporangium before cleavage of the protoplasm, and the paired nuclei are held together by a common nuclear cap (fig. 21). As McCranie (1942) pointed out, from one to several nuclei may be included in a single spore at cleavage. As a rule, however, only two nuclei are contained within each spore. When these spores emerge from a resistant sporangium of *Cystogenes,* they possess the same number of flagella as nuclei, usually two. A biflagellate spore from the resistant sporangium of *Cystogenes* is shown in figure 20, which was taken with a phase microscope. From one to six flagella have been noted upon a single spore. This is directly correlated with the size of the spore and the number of nuclei that it contains. From this point, only the typical biflagellate spores will be discussed.

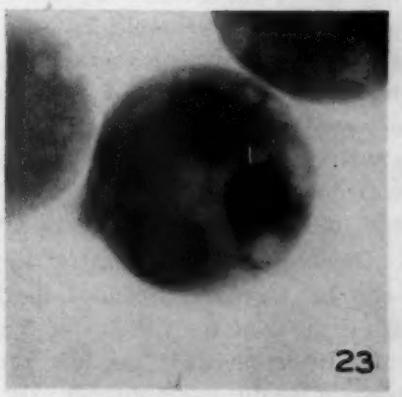
About two hours are required for the spores to form after the mature resistant sporangia are placed in water. Because of the pairing of the nuclei, just half the expected number of spores emerge from a sporangium. These binucleate, biflagellate spores soon lose their flagella and become cysts. After the spores have become cysts, the common nuclear cap disappears and the two nuclei become free in the cytoplasm (fig. 22). At this time the only haploid mitotic division in the life cycle takes place, and the two nuclei in the cyst are increased to four. Although nuclear caps are again formed, they now remain discrete (fig. 23), and the nuclei do not pair. Planes of

cleavage are formed between the nuclei and four gametes are produced within each cyst. It takes one to two hours from cyst formation to the emerging of the gametes from the cysts. The gametes may fuse soon thereafter, forming zygotes. The diploid nucleus of the zygote is larger than the haploid nuclei of the cysts. The differences in the sizes of the diploid and









FIGS. 20–23. Approximately × 2660. FIG. 20. Biflagellate spore from resistant sporangium of *A. cystogenus* (Burma 1B). Taken with phase microscope. FIG. 21. Two nuclei of young cyst with common nuclear cap. FIG. 22. Two nuclei free in cytoplasm of cyst just before division. Nuclear cap has disappeared. FIG. 23. Cyst just after gametogenesis. Nuclear caps have reformed but remain discrete for each of the four nuclei.

haploid nuclei correspond with the differences found by Kniep (1930). The haploid phase of *Cystogenes* is about two hours long, if one does not include the time for the reduction divisions. The times for resistant sporangium and cyst germination agree in general with the times reported by Emerson (1938).

Whether or not two gametes from one cyst will fuse with the other two from the same cyst and thus indicate that the two original paired nuclei in the spore from the resistant sporangium are of different sexes has not been determined. By inference it is probable that the gametes in the cyst are differentiated sexually. The cyst of *Cystogenes* is homologous to the gametophytic plant of *Euallomyces* in that both contain haploid nuclei and arise from the spores produced by the resistant sporangia of the sporophytes. The gametophytic plant of *Euallomyces* is homothallic, and it is probably safe to assume that the cyst of *Cystogenes* is also homothallic. The pairing of the nuclei in the resistant sporangium lends weight to this supposition. That the paired nuclei in the resistant sporangium are of different sexes physiologically is the only reason that the writer can think of for their pairing. Even though odd numbers of nuclei are occasionally included in a single spore, it should not detract from the argument that the nuclei may be sexually different, for it is the rule rather than the exception that several male gametes are usually attracted to a female gamete, although only one accomplishes fertilization.

It should also be noted that the biflagellate condition of the spores from the resistant sporangia of *Cystogenes* is different from that of *Saprolegnia,* for example. In *Saprolegnia* the uninucleate spore is biflagellate, but in *Cystogenes* a biflagellate spore must also be binucleate; and when the number of nuclei is increased, the number of flagella is increased in the same amount. In rare instances where only one nucleus is included in a spore from the resistant sporangium of *Cystogenes,* the spore has only one flagellum. In this case the nucleus also divides only once, and only two gametes arise from the cyst.

Discussion. The demonstration of meiosis and the study of the chromosomes in *Allomyces* included in the present work offer conclusive cytological proof of the validity of Kniep's interpretation of *Euallomyces,* in which he emphasized the fact that the zygote did not enter a resting stage—a condition considered very rare in the lower fungi—, in which he pointed out that this sexual reproduction was the most primitive in the filamentous fungi, and in which he noted the uniqueness of the alternation of equal and separate haploid and diploid generations. By direct cytological evidence, the present work, in confirming Kniep's observations, also proves fallacious the long accepted belief that the nuclei in all vegetative parts of the filamentous fungi are haploid and that the zygote alone is diploid. An even greater departure from this prevalent belief is provided by the present study of the *Cystogenes* life cycle, which is so predominantly diploid that only one division of haploid nuclei occurs in the whole cycle.

Although there are no counterparts of the Allomyces life cycles known outside of the Blastocladiales in other groups of filamentous fungi, similar life cycles are found in some of the algae; for example, *Ulva* and *Cladophora* have cycles similar to *Euallomyces,* while the reduction of the gametophytic phase in the Cyclosporales of the brown algae is similar to that found in the life cycle of *Cystogenes,* and the omission of the haplophase under certain conditions in *Ectocarpus* is comparable to the omission of sexual stages in *Brachyallomyces.* Schussnig (1930) summarized the work of several investigators demonstrating the existence of diploid plants in the green algae. He also pointed out that where diploid and haploid plants were found the zygote did not enter a resting stage. This condition is analogous to that found in *Allomyces.* Where equal and separate haploid and diploid plants exist, it is necessary that there be a delay of gametogenesis after reduction of chromosomes and that there be a delay of meiosis after fusion of gametic nuclei.

The life cycles of *Allomyces* certainly offer great potentialities for genetic research. So far as the writer knows, the variation and interplay of these life cycles afford certain tools for the study of inheritance that do not exist in any other well known organism. It is possible in *Allomyces* to get a completely homozygous diploid plant by selfing the gametophyte which grew from a uninucleate haploid spore. The gametophytes are also cross-fertile. In some respects the potentialities that *Allomyces* offers for the study of gene relation to enzyme systems are as great as those of *Neurospora.* At best the nuclei in *Neurospora,* with the exception of the fusion nucleus, are diploid only as a dicaryon, but in *Allomyces* there are haploid and truly diploid plants. This diploidy in *Allomyces* will make possible the study of dominance and cumulative effects which are not open to investigation in *Neurospora.* Although it is admitted that the influence of the genetic complement of both nuclei is exerted in a dicaryon, it would be a matter of conjecture as to how equally the effects of both genotypes in a dicaryon might be expressed in a plant.

The ease in handling *Allomyces* is one of its greatest assets. It grows best at room temperature and can be grown in quantity in liquid or on solid media. By transferring old cultures to fresh agar slants either the gametophytic or the sporophytic stages can be prolonged indefinitely, or a culture can be kept for years by simply drying the resistant sporangia. Since it is possible to time accurately the meiotic phases in *Allomyces,* material for genetic studies could be irradiated at the most effective point in meiosis, if this proved favorable. Sparrow (1948) has found that the cells of some organisms are much more sensitive to irradiation during meiosis than at other times.

Now that the practicability of dependable cytological studies within the group has been demonstrated, the value of *Allomyces* for cytogenetic and cytotaxonomic research on a scale similar to some of the studies made in the higher plants and animals is readily apparent. The covering effects of polyploidy have hindered previous investigation of the genetics of *Allomyces,* but now that it is possible to determine the chromosome number of the strain used this difficulty can be eliminated. Although polyploidy is known in some of the algae, *Allomyces* is, so far as the writer knows, the only microorganism that can be handled experimentally to utilize this knowledge.

SUMMARY

1. This investigation of chromosome reduction in *Allomyces* represents the first detailed study of meiosis in the *Phycomycetes.*

2. While previous workers had indicated the approximate position of meiosis in the subgenus *Euallomyces,* the present cytological study shows that the two meiotic divisions occur in the germinating resistant sporangia.

3. In the subgenus *Cystogenes,* in which nothing was known regarding chromosome behavior, meiosis also takes place in the germinating resistant sporangia. This subgenus is shown to be predominantly diploid with only one division of haploid nuclei in the entire life cycle.

4. In *Brachyallomyces,* a subgenus whose nuclear behavior was also unknown, the nuclear divisions in the resistant sporangia are mitotic rather than meiotic, and, as a consequence, the sexual phase is omitted from the life cycle.

5. The Euallomyces life cycle is compared in detail with the Cystogenes and Brachyallomyces cycles.

6. Some of the phenomena of maturation and germination of the resistant sporangia of *Allomyces* are described. The cytoplasmic and nuclear changes in the maturing sporangia are correlated with their ability to germinate. The effects of temperature and age are found to be important factors in the germination of resistant sporangia.

7. Although meiosis in *Allomyces* follows the general pattern of most organisms, the reduction divisions exhibit certain points of interest, such as the intranuclear divisions, the large nucleolus, and the late prophase of meiosis in which the nuclei are arrested until germination of resistant sporangia begins.

8. The chromosome numbers are given for certain isolates, and polyploidy is reported in two species.

9. By direct cytological evidence of chromosome numbers, this work

confirms Kniep's belief that filamentous fungi occur in which the true diploid condition exists in vegetative hyphae.

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MONOGRAPH OF THE GENUS ANACOLIA[1]

SEVILLE FLOWERS

ANACOLIA Schimp. Syn. (Ed. 2), 513, 1876, emend. Holz. Bryol. 7: 29. 1904.

ANACOLIUM Schimp. Syn. (Ed. 1), 421. 1860.

Plants in dense or loose tufts, yellowish-green above, usually densely clothed with felt-like, densely prickly, roughened or sometimes smooth, ferruginous rhizoids, at least at the base. Stems monopodially or dichotomously branched, erect or ascending from prostrate main stems 3–20 cm. long, 8-angled and roughly papillose, central strand present, outer rind of 2–4 rows of smaller, thick-walled colored cells. Leaves 8-ranked, closely appressed and imbricated when dry, straight, erecto-patent or recurved spreading when moist; mostly narrowly lanceolate from an ovate base sometimes broader or narrower above, base concave with a strong fold on either side, deeply channelled above; costa stout, percurrent to long spinulose excurrent, guides in 1, 2, or partially 3 rows with a dorsal sterid band, with or without some ventral sterids; margins revolute half the length of the leaf or more, margin 1-2-stratose and doubly serrate in upper half; upper lamina unistratose to variably bistratose. Upper cells often various in the same leaf, mostly oblong to linear, some often quadrate, strongly papillose to nearly smooth, all thick-walled 3–8 μ wide; basal cells usually shorter and broader, sometimes linear near costa, firm and thick-walled. Dioicous. Perigonia terminal, becoming lateral by innovation, bud-like, bracts usually very narrowly lanceolate to linear from a very broadly ovate, concave base, usually colored. Perichaetium terminal, becoming lateral by innovation perichaetial leaves not much different from stem leaves, usually slightly shorter; sporophyte terminal, soon appearing lateral by innovation; seta 2–15 mm. long, straight or curved; capsule globose, ovoid or shortly oblong-cylindrical, 2–3 mm. long leptodermous, rugulose when dry; neck lacking or very small; mouth small, peristome lacking or composed of 16 short, lanceolate, irregular or imperfect teeth arising half their length below the mouth, fragile, usually falling early, endostome rare, very faint; lid low convex, saucer-shaped to conic-obtuse; spores globose to reniform, 17–32 μ, with rather large blunt or warty papillae. Type species *A. webbii*. First discovered by Webb on rocks in the mountains, Los Organos, above Tenerife.

A small genus of interesting geographical distribution. There are three species in the western hemisphere extending from Alaska almost continuously to Chile. *Anacolia menziesii* extends from Alaska to southern California, in the coastal mountains and eastward into northern Idaho, western Montana, Wyoming and adjacent Canada. *A. intertexta* ranges from Chihuahua through the central part of Mexico to Guatemala. *A. laevisphaera* has a very long range extending from Colorado and Arizona more or less

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continuously southward to Chile. In South America it is restricted to the Andes Mountains. It occurs as a disjunct on the Island of Juan Fernández, in Abyssinia and near Madura in southern India.

Four species are inhabitants of the eastern hemisphere. *Anacolia webbii* has an interesting distribution in the western Mediterranean region including Sicily, Corsica, Spain, Portugal, Algeria, Morocco, the Canary and Madiera Islands. *A. cameruniae* occurs on Mt. Cameroons at the extreme southeastern tip of Nigeria. *A. abyssinica* occurs in Abyssinia and Eritrea. *A. sinensis* is known from Setschwan and Yünnan provinces in southwestern China.

KEY TO SPECIES

Leaf cells mostly with prominent papillae on both sides; seta mostly short, 2–3 mm. long (except in one form); peristome lacking.
- Leaves bistratose in upper portion; cells papillose at both ends, seta straight.
  - Inner basal cells linear to oblong; leaves recurved to faclate, coarsely serrate, 3–6.5 mm. long ..... 1. *A. laevisphaera*
  - Inner basal cells oblong to quadrate; leaves mostly straight, slightly if at all recurved, moderately serrate, mostly 2.5–3.5 mm. long ..... 2. *A. webbii*
- Leaves unistratose above.
  - Inner basal cells linear; papillae on the ends of the cells; leaves flexuose, not appressed when dry ..... 3. *A. cameruniae*
  - Inner basal cells quadrate to shortly rectangular; papillae in the center of the cells; leaves straight, more or less appressed when dry.
    - Leaves mostly 2–3.5 mm. long, moderately to strongly serrate above.
      - Central strand of stem small, $\frac{1}{6}$ the diameter of the stem or less; seta short and curved, capsule often projecting laterally from between the leaves.
        - Leaves narrowly lanceolate from an ovate base, 2.5–3 mm. long, 0.4–0.8 mm. wide ..... 4. *A. intertexta*
        - Leaves broadly ovate-lanceolate, 2–2.5 mm. long, 0.7–0.9 mm. wide ..... 4a. var. *latifolia*
      - Central strand large, about $\frac{1}{4}$ the diameter of the stem or larger ..... 5. *A. abyssinica*
    - Leaves mostly larger, 3–5 mm. long, moderately serrulate to subentire above, central strand of the stem small, $\frac{1}{6}$ the diameter of the stem or less ..... 6. *A. sinensis*

Leaf cells weekly papillose at both ends on the upper surface only, often smooth; seta longer, 5–10 mm. long; peristome present but usually fragile and falling early.
- Leaves narrowly lanceolate from an ovate base, 2.5–3.5 mm. long, 0.5–0.6 mm. wide at the base, costa percurrent to long excurrent.
  - Capsules ovoid to globose, spores 28–32 μ ..... 7. *A. menziesii*
  - Capsules oblong to subcylindric, spores 18–22 μ ..... 7a. var. *baueri*
- Leaves shorter, more nearly ovate-lanceolate, 1.5–2 mm. long, 0.55–0.65 mm. wide at the base, costa percurrent to shortly excurrent ..... 7[1]. forma *brevifolia*
- Leaves longer, mostly subulate from an ovate base, 3.5–5 mm. long, 0.6–0.8 mm. wide at the base, costa usually exceedingly long excurrent, capsule as in the species ..... 7[2]. forma *grandifolia*

1. ANACOLIA LAEVISPHAERA (Tayl.), (figs. 1–15 and 65). Flowers, in Grout's N. A. Moss Fl. vol. II, p. 155. 1935.

Glyphocarpa laevisphaera Taylor, Lond. Jour. Bot. 5: 56. 1846.
Bartramia subsessilis Taylor, Lond. Jour. Bot. 6: 334. 1847.
B. laevisphaera C.M. Syn. I. 506. 1849.
Glyphocarpus taylori Hampe, Flora 45: 453. 1862.
Glyphocarpa taylori Hampe, Ann. Sci. Nat., Bot. Ser. V. 3: 370. 1865.
Glyphocarpus subsessilis (Tayl.) Jaeg. Jahresb. St. Gall. naturwiss. Gessell. 62. 1873–74. Ad. I. 526. 1873–74.
Anacolia abyssinica Schimp. Syn. Ed. II, 514. 1876.
A. subsessilis (Tayl.) Broth. in Engler & Prantl Ed. I. 634. 1904.
A. subsessilis var. *brevifolia* Broth., in Skottsb. Nat. Hist. of Juan Fernández and Easter Isl. 2: 425. 1924.
A. subsessilis var. *densiretis* Ther., Rev. Bryol. ii, 5: 104. 1932.

Plants loosely tufted, yellowish-green, often tinged with brown, occasionally dull green. Stems erect or ascending, often slightly curved at the tips, 1–5 cm. tall, branches erect or slightly spreading, monopodial or dichotomous, occasionally 3–4-whorled, central strand present, $\frac{1}{6}$–$\frac{1}{4}$ the diameter of the stem; rhizoids few or dense, reddish-brown. Leaves variable, 2–6.5 mm. long, ranging from lanceolate-linear from an ovate base, usually recurved, falcate or widely spreading to smaller triangular-lanceolate, straight and erecto-patent forms; when dry not greatly changed in shape, erect and appressed, the tips often spreading and the comal tuft usually curved to one side; base concave with a prominent fold on each side, channelled above; costa about, 60–100 μ wide near the base, more or less toothed on the back, excurrent into a stout or slender spinulose awn, short or long, guides in 1–2 rows, dorsal sterid band strong, often gradually merging with the bi-tristratose upper lamina; margins revolute for $\frac{1}{2}$–$\frac{3}{4}$ the leaf length, often merely recurved at the base, very coarsely doubly serrate above, entire or dentate below; upper lamina mostly bistratose, in some plants 3–4-stratose adjacent to the costa, becoming unistratose toward the base; upper cells oblong to linear, 3–7 μ wide, up to 46μ long, papillose at both ends, marginal cells usually shorter, thicker-walled and more highly colored; cells of the marginal teeth much larger, up to 12 μ wide and with very thick walls; inner basal cells linear, only slightly wider than the upper cells, up to 112 μ long; basal marginal cells becoming much wider and shorter, mostly oblong, extreme marginal ones often quadrate, up to 20 μ wide.

Dioicous. Perigonium terminal, bud-like, rather small, becoming lateral by innovation, sometimes subtended by 2–3 whorled branches, leaves broad at the base, abruptly narrowed to a slender, straight or flexuous upper portion, costa slender, percurrent to excurrent. Perichaetium terminal, becoming lateral by innovation or subtended by 2–3 whorled branches, leaves similar to those of the stem, inner ones shorter, outer ones often with very long aristate points. Sporophyte terminal or lateral by innovation; seta short, straight, less than 1 cm. long, reddish-brown; capsule nearly spherical, 2–3 mm. in diameter, reddish-brown when ripe, rugulose when dry, neck lacking, mouth small; exothecial cells quadrate to polygonal, several rows below the mouth transversely elongated, thicker-walled and darker in color; peristome lacking; lid low convex. Spores spherical to shortly ovoid, often flattened on one side, 23–28 μ, coarsely roughened with large wart-like papil-

lae. Type locality in Ecuador, Andes mountains, near summit of Mt. Pichincha. Type seen.

Mostly on dry or damp soil, often in crevices or talus, usually in the shade of forest regions; mostly between 3,000 and 12,000 feet elevation. Colorado, New Mexico, Arizona, Mexico, Guatemala, Colombia, Venezuela, Ecuador, Peru, Bolivia, Chili and western Argentina; disjunct on Juan Fernández Island, in southern India near Madura and in Abyssinia.

Specimens examined: United States: Miller, R. B. 1220. Kept damp by spray, Boulder Falls, 8,000 feet. pH 8, Colorado; Arsène 18483, 18490. Porvenier Canyon; 18771. Thunderbird Ranch; 18902. Gallinas Canyon and 18646. Las Vegas, New Mexico; Bartram, E. B., Mosses of Santa Cruz County, Arizona 1212, 1212a, 1233. Rock clefts, 8,000 feet, Baldy Trail, Santa Rita mountains; Mosses of So. Arizona 110, 1463. Shaded Rock face, 6,500 feet, White House Canyon, Santa Rita Mountains. Holzinger, Musc. Acro. Bor. Amer. et Eur. 551, Arizona. Mexico: Mexía, Ynes, Pl. of Mexico 2610. Chichuahua; Orcut, C. R., Mosses of Mexico 3803. Parres, Federal Distr.; 6740, 6779. Mineral del Chico, State of Hidalgo; 6984. sine loco. Pringle, C. G. Plantae Mexicanae 10513. Base of trees, Cima, 10,000 feet, Federal Distr.; Fr. Amable, 1821. Cuantziro, 3,200 m., Feb. 1931. Bro. Arsène, Pl. of Mexico 4729. Esperanzo, 2,400 M., vicinity of Puebla, State of Puebla; 4938, 4939. Hacienda Batán, 2,120 M., l. loc.; 7908. Vicinity of Morelia, 2,000 M., State of Michoacán; 7963. Jesús del Monte, 2100 M., l. loc. Guatemala; Standley, Pl. of Guatemala 84170. Damp shaded banks, Dept. Quezaltenango, 2700–2800 M. Colombia: Mutis, J. C. Pl. of Colombia 2085. Wier 291, 293, 295. Andes Bogotensis, Bogotá, Fusagasuga, 8,000 feet; 195, 217. Boquerón, 8,500 feet. Apollinaire 381. Andes Bogotens. La Mesa pr. Bogotá, Majo 1906; 382. Andes Bogotens., San Cristobal, pr. Bogotá, Majo 1906; 676. Colombia: Bogotá, 1905 (all as *A. subsessilis*). Venezuela: Pittier, H., Mosses of Venezuela 12885a. Wet ground between Tobay and Macuraba, Mérida. Ecuador: Jameson 30, 31. Andes of Quito, near summit of Pichincha, 1847 (in part as *Glyphocarpa laevisphaera* Taylor, Type, and in part as *Bartramia subsessilis* Taylor, also marked Type). Spruce, Mus. Amazon. et Andini 404, 405. Andes Quitensis, Villavincencio, M. 56. 57. Banks of River Napo. Meyer, Pflanzen aus dem Hochland von Ecuador 5426. El Altar: Paramo-region, bei 4000 m. 1903. VII. (as *Bartramia subsessilis*). Peru: Cook and Gilbert, Pl. of Peru 479, 504, 771a. Ollantaytambo, alt. about 3,000 M. Hererra, F. L., Pl. of Peru 442. Valle del Apurimac, Vicinity of Mallepata, 2,800 M.; 1464a. Urubamba Valley near Gucay, 3,000 M.; Diehl, A., Pl. of Peru 2549, no other data. Chili: Stevenson, A. W., Mosses of Chili, vicinity of Santiago. Bro. Claude-Joseph, Pl. of Chili 5783. Ternuco. Argentina: Hosseus, C. C., 318, 330, 567. Prov. Córdoba, Cerro Uritorco, lat. austr. 2; 1750 M. A single stem of *A. laevisphaera* of unquestioned identity was found in a packet of Dusen's No. 600 (*Anacolia auricolor*), Patagonia occ. in valle fluminis, Aysen in rupibus, Feb. 23, 1897. It represents the known southernmost limit of this species. Juan Fernández Island: C. Skottsberg Svenska Pacific-expeditionen 1916–1917. No. 201. (as var. *brevifolia* Broth. Type) Mas Afuera, Feb. 11, 1917; No. 202. (as var. *brevifolia* Broth.) Mas Afuera, Casas de Papae, 200 m. s. m., Feb. 19, 1917; No. 210. Mas Afuera, ad rupes, 590 m.s.m. Dec. 3, 1916; 360 Mas a Tierra, ca. 600 m.s.m. Dec. 25, 1916. Abyssinia: Schimper, without number (as *Glyphocarpa webbii* Wils); Schimperi iter Abyssinicum 441. in part with *Bartramia brachypus* Bruch (as *Bartramia* (*Glyphocarpa*) *webbii* Mtgne). In monte Silke ad limites arborum et fructicum locis rupestribus uliginosis ad terram. U. i. 1842. d. 16 Febr. 1840. Some samples are entirely *Bartramia* (*Vaginella*) *brachypus* B. & S. while others are entirely *Anacolia laevisphaera*. India: Prov. Madas. Foreau at Roine, Musci Madurensis, Indies Merid, No. 51. Kodiakanal, on ground (disjunct).

A species of great variability in stature, and size and shape of the leaves. Some of these variations are shown in the illustrations. The largest and more robust forms grow in the tropics and subtropics at rather high alti-

tudes while at the northern limit of the range in Colorado, New Mexico and Arizona, and at the southern limit in Argentina the plants are much smaller and more strict in habit, the leaves often very narrow.

The bistratose upper lamina, linear inner basal cells and strong papillae at both ends of the cells on both sides of the leaf are outstanding features common to all forms. The upper leaf cells are typically oblong to sublinear, but in some plants shortly rectangular cells may predominate while the basal cells are shorter than typical in being barely linear as shown in Fig. 13.

The costa structure varies somewhat. The ventral superficial cells are small and immediately below them there are usually 1–2 rows of thick-walled, enlarged cells (guides) with few or no sterids standing ventral to them. The dorsal sterid strand is very strong and usually colored, and the dorsal superficial cells small and fairly thick-walled. The stem cross section shows a rather large central strand comprising $\frac{1}{6}$–$\frac{1}{4}$ the stem diameter although Stevenson's large plant from Chile shows some stems with a very large strand up to $\frac{1}{2}$ the stem diameter. Diehl's equally large specimen from Peru has only a comparatively small strand about $\frac{1}{6}$ the stem diameter.

Brotherus named a plant from Mas Afuera, Juan Fernández (C. Skottsberg 201, 202) var. *brevifolia*. I can find nothing about it to distinguish it from the commonest forms. The leaves are 3–4 mm. long, 0.5–0.7 mm. wide at the base. Many other specimens of the species have much shorter and narrower leaves and as the varietal name implies a short leaf for the Juan Fernández plant it would lead to confusion among a large number of forms included within the range of the species.

Var. *densiretis* Ther. also falls within the range of the species. It is a small form with narrower leaves, less plicate, and smaller areolation. It is much like plants from the northern and southern extremities of the geographical range.

Forma **longiseta** forma. nov. Formis majuscula; folia angustata, recurvata, 5–5.5 mm. longa, in basi 0.8 mm. lata. Seta circa 1.8 cm. longa, excedens folia perichaetialis.

Plants of the larger type, leaves large, long and slenderly recurved, up to 5.5 mm. long, 0.8 mm. wide at the base. Costa percurrent in many leaves, shortly excurrent in the comal ones. Seta long, far exceeding the pericheatial leaves and usually exceeding the tips of the current season's growth, about 1.8 cm. long.

Chili, Ternuco. Bro. Claude-Joseph, Pl. of Chili 5783. Type in the U. S. National Herbarium. This specimen has about a dozen good setae of immature sporophytes some of which are sufficiently well advanced to show the globose-ovoid shape. The leaves are similar to those shown in fig. 65.

1a. var. **parvifolia** nomen nov. (*A. subsessilis* var. *brevifolia* Herz. Fedde, Repert. 45: 47. 1938, non Broth.) Differt a typo minutie omnium partium

foliis brevioribus latioribusque. (original description, l.c.). Peru: Cordillera Blanca; Gletschervorfeld oberhalb Lager Copachica, 4400 m. leg. Lucas, 1932. I have not seen this plant. A request to see the type was ignored. From the above description I should judge it to be about the same as Brotherus' variety of the same name.

1b. var. NIGROVIRIDIS Card. Rev. Bryol. 37: 4. 1910. Plants smaller than the type, somewhat densely tufted, stems up to 4 cm. long, erect, blackish below, yellowish-green only at the tips, leaves patent, only slightly recurved, diverging at about a 40° angle, 3–3.5 mm. long, 0.4–0.55 mm. wide at the base, lower ones blackish-green, costa and marginal teeth darker. Cells very thick-walled, papillae low and rounded.

Pringle, Pl. Mexicanae 15207, Cima, 10,000 feet, Federal District, Mexico. Barnes and Land, Pl. Mexicanae, Boundary between States Morales and Mexico: La Cima, 9,900 feet, damp bank, railroad cut. 1908. Fr. Amable no. 1813. Mexico: Cuantziro, 3,200 m.

2. ANACOLIA WEBBII (Mont.), figs. 16–24. Schimp. Syn. II, p. 513, 1876.
Glyphocarpus webbii Mont. in Ann. sc. nat. II. Series IX, p. 56. 1838. Pl. cell. Canar., p. 28, t. 2, f. 2. 1840; Syll. p. 291. 1856.
Bartramia (*Eubartramia*) *webbii* C. Mull. Syn. I. p. 504. 1849.
Bartramia granatensis Schimp. Coroll. p. 85. 1856.

Plants in loose or rather dense tufts; stems 2–6 cm. tall, dichotomously branched, erect or ascending from a prostrate lower portion, straight or slightly curved, more or less parallel; current season's growth usually yellowish-green (sometimes dull green), preceding season's growth usually covered with a dense felt of ferruginous rhizoids, this occasionally poorly developed. Cross section showing a rather small central strand $\frac{1}{6}$–$\frac{1}{3}$ the total stem diameter.

Leaves 2.5–3.5 mm. long, 0.5–0.8 mm. wide at base, typically slenderly and evenly triangular lanceolate from a broader ovate, concave base, channelled above, when dry closely imbricated, not greatly changed, costae very prominent at backs; when moist spreading at about a 45° angle or less, mainly straight, sometimes slightly curved backward or inward, margins recurved to revolute $\frac{1}{3}$–$\frac{1}{2}$ length of leaf; upper margins moderately doubly serrate, becoming dentate or entire below; base with two large lateral folds and sometimes with smaller plicae between; costa very stout, 75–105 μ wide at base, 45–76 μ wide near apex, very prominent and projecting at the back, excurrent from the gradually diminishing lamina and forming a relatively short or long arista up to 1 mm. long in larger leaves. Cross section showing 1–2 or partially 3 rows of guides, 1–2 rows of ventral sterids and a larger area of dorsal sterids. Upper lamina bistratose, becoming unistratose near junction with broader base; upper median cells typically oblong to linear, 3–5 × 12–30 μ with a few shorter ones, all thick-walled, papillose at both ends, the papillae sometimes very coarse and prominent in some plants or scarcely discernable except in cross sections in others; marginal cells thicker-walled and more highly colored, cells of the teeth larger than their neighbors but only slightly so in some leaves, closely set to rather distant; basal cells becoming shorter and broader, oblong, quadrate and transversely elongated, 8–14 μ wide, one shape may predominate, variable in different leaves of the same stem or of different plants; basal marginal cells still shorter, often predominantly transversely elongated.

Dioicous. Perigonium terminal, appearing lateral by innovation or axillary with 2–3 branches subtending it, bud-like, spherical to ovate; perigonial leaves with a very broadly concave, spoon-shaped, clasping, base, ovate to nearly orbicular, suddenly narrowed above to a linear or lanceolate, bistratose apex, outer leaves with long straight or flexuose aristae, basal cells broad, oblong to hexagonal, pellucid, often reddish; antheridia large, about 0.7 mm. long, reddish when old, paraphyses numerous, exceeding the antheridia. Perichaetia terminal and soon subtended by 1–3 branches or lateral by innovation, usually small, slender and often inconspicuous, outer leaves more broadly clasping at the base, the inner ones becoming narrower, the base finally scarcely differentiated, more or less evenly tapered, linear-lanceolate, the basal cells irregularly oblong to fusiform, pellucid or colored at the insertion; archegonia mostly few, in some plants moderately dense, about 0.7 mm. long, paraphyses few, linear, usually quite short. Sporophyte terminal and subtended by 1–3 branches or lateral by innovation; seta very short, about 1 mm. long, straight, thick and dark reddish-brown; capsule erect, subglobose, about 2 mm. long, yellowish to reddish-brown, rugulose when dry, mouth rather small, reddish; exothecial cells 4–6-sided, mostly shortly rectangular, some nearly isodiametric, thin-walled and pellucid, often inflated and roundish, 33–66 μ wide, 4–6 rows below the mouth compressed and transversely elongated, thicker-walled, stomata few in the base, up to 33 μ long; lid low convex, orange-red, annulus lacking. Spores ovoid or reniform, 20–26 μ long, reddish-brown, beset with large low papillae; calyptra small, high conic, cuculate. Type locality Tenerife, Los Organos.

Habitat: usually among rocks, in crevices or ledges, also on soil and humus.

Distribution: Canary and Madiera Islands, Portugal, Spain, Corsica, Sicily, Algeria and Morocco.

Specimens examined: E. Bourgeau, Pl. Canarienses 1586, Teneriffa: Los Organos, in rupibus; E. Bornmüller, Kryptogamae exsiccatae 1090, Insulae Canarienses (Gran Canaria) in jugis alpinis, Rogue de Sancillo; and Flora exsicc. Maderensis 219. Pico Grande, 13-1400 m.; Husnot, Musci Galliae 237 and Pl. Canarienses 120, Sur les rochers de Los Organos, audessus de la Villa Teneriffe; Möller, Canarie; Camus, Agua Manza; A. Tullgen, Canaren, Agua Manza, June 28, 1896 and Tenerife: Agua Garcia, July 21, 1896; N. Bryhn, Bryophyta canariensia. Tenerife: Agua Garcia, 700 m., May 5, 1908; P. Barker-Webb, Herb. Florae Canariensis (as Glyphocarpus); O. Gelert, Gran Canaria, Tejeda, 3000 feet, May 25, 1897; F. B. Borgesen: Pl. canariensis 210, 211. Tenerife. R. Fritze, Plantae Maderenses, 4000 feet, Jan. 25, 1880; Luisier: Mousses de Madère: Chemin du Grad Curral; Bryotheca iberica, Portugal: Ayselo (Vimino, nord du Portugal); Salamanca, Spain: Sin les rochers ensoleillés, aux bords du Tormes; Richards, Spain: Sierra Navada, Ledges of moist shale rocks 5–600 feet, Upper Valley of R. Genil: R. Fritze, Hispania austr.; in valle "Genilthal," Sierrae Nevadae, 6000 feet. 1873; Nicholson, Flora Sicula, Acqua della Batata, prope Ficuzza ad rupes arenaceas madidas; Dixon & Nicholson. Sicilia, Ficuzza. May 3, 1914; Lojacono Pojero, In Insula Sicilia, Italiae, ad rupes arenaceas madefactas, in latioribus "Acqua della Balata," 11 Aprilis 1889; E. Bauer, Musc. Eur. Exsicc. 1659b, Sicilien: Balata, Ficuzze, auf einer Felswand; 456, Corsica: Corte; im Forêt de Captotile in der Schlucht des Tavignano auf nassen Granitfelsen, etwa 1100 m.s.m.; Trotter: Calve, Corsica. Vaucher, Atlas, Morocco, Ourika. 1909: Herbier Ed. Jeanpert: Atlas (as Glyphocarpus).

This species is uniform in its basic characters and the collections exam-

ined show little deviation from them. Such variations as exist are closely intergraded and perhaps traceable to habitat conditions. Plants of short stature often have shoots with several short, rather closely disposed branches giving the plant as a whole a more compact tufted appearance. Taller forms may have long simple or sparingly branched shoots.

In some plants the leaves may be quite uniform in shape and size but in others they may vary considerably in both these features. It is not uncommon to find a strong contrast in the leaves of the same stem. The chief variations are the degree of dilation of the base, the narrowness of the upper lamina and the variable length and stoutness of the arista. The latter is usually short, thick and stout, but occasionally it may be relatively slender and extend as much as 1 mm. beyond its junction with the lamina. The areolation also varies both in different leaves of the same plant and in different plants. Often the cells of the upper lamina show a mixture of various shapes but usually one shape predominates. In the basal cells the same condition obtains. The serration of the upper margin is usually moderate, occasionally weak, distant and vaguely dentate, but never as coarse as occurs in *Anacolia laevisphaera* or *A. intertexta*. The apical or comal leaves are frequently shorter and with shorter points than the lower leaves. In some cases the papillae are not apparent in the surface view but good cross sections of the leaves show them. The bistratose area of the upper lamina generally tapers off into vague lines toward the base of the upper lanceolate portion while the broader ovate base is unistratose throughout. The cross sections of the costa show 1–2 or partially 3 rows of thick-walled guides according to the level of the leaf examined. Most collections seen are sterile and predominantly with archegonia. The perichatia are usually very slender and inconspicuous.

3. ANACOLIA CAMERUNIAE Dixon, Annal. Bryologici 6: 25. 1933.

Robustiuscula; folia falcatula, sicca laxiuscule flexuosa, haud adpressa. Ab *A. subsessili* (Tayl.) differt foliis inferne angustioribus, magis pellucidis, cellulis superioribus longioribus, minus opacis, humilius papillosis, unistratosis. Ab omnibus speciebus reliquis aut cellulis basilaribus linearibus, haud subquadratis, aut papillis cellularum terminalibus haud medianis, differt.

Fructus ignotus.

Hab. Cave, 11,000 ft. alt., (23, type; 24a). (M. Steele 1932). Nigeria: Mt. Cameroon.

"Distinct from nearly all the species in the leaves flexuose and not appressed when dry; in *A. subsessilis* the same foliation sometimes occurs, but the upper cells are bi-stratose and the lamina therefore is very opaque. All the other species differ either in having the papillae in the middle of the lumen or the basal cells subquadrate."

"In most species the stems are densely tomentose with short radicles; in the present plant, especially on 24a, they are furnished here and there with tufts of extremely long rhizoidal filaments, often considerably longer

than the leaves, arising from the stem or leaf-bases; of a deep purple brown, with smooth, not papillose walls, almost unbranched, but here and there furnished with very short, delicate lateral ramuli, and with occasional small nodules (from which these ramuli may perhaps arise), and internally with very oblique partitions."

"The dentations of the leaf subula are usually rather markedly pellucid, which appears a frequent occurence in this genus." The original description and above notes are quoted from Dixon, l.c. I have not seen this plant. Requests to see the type specimens were ignored.

4. ANACOLIA INTERTEXTA (Schimp.), figs. 33–49. Jaeg. Ad. II. p. 699. 1877–78.

Bartramia (*Glyphocarpa*) *intertexta* Schimp. in Herb. Schlechtend.

B. intertexta (Schimp.) C. M. Syn. I. pp. p. 503. 1849.

B. lamprocarpa Schimp. in herb. Mus. Paris.

Glyphocarpa intertexta (Schimp.) Besch. Mem. Soc. Sci. nat. de Cherbourg 16: 202. 1871.

Bartramia subintertexta C. M. ined. 1898.

Anacolia mexicana Broth. in herb.

Plants in loose or rather dense tufts, erect or sometimes matted below with prostrate main stems and ascending branches. Stems up to 8 cm. long and probably longer, branches both monopodial and dichotomous, tips often slightly curved when dry, mostly yellowish-green, occasionally dull green, especially when young, lower portion with densely interwoven, felt-like, ferruginous rhizoids, occasionally poorly developed in some plants. In cross section stem roundish, 8-angled (sometimes imperfectly so), central strand small, $\frac{1}{8}$–$\frac{1}{6}$ of total stem diameter, cortex thin or thick-walled; yellowish or reddish, rind of 3–4 layers of smaller very thick-walled cells, dark or blackish, surface of stem rough.

When dry leaves appressed and imbricated at base, not greatly changed, the halves of the laminae often conduplicate, comal leaves often all curving in the same direction, costa very prominent at the back; when moist spreading at about a 45° angle, occasionally more; predominantly 2.5–3.5 mm. long, extreme basal ones often much shorter and broader; typically with a very concave, ovate base, narrowed above to a triangular-lanceolate or long lanceolate-linear, channelled apex; sometimes the entire leaf is more or less long triangular-lanceolate and evenly tapered from the base; base very concave with two large folds on either side and often with two smaller plicae between; costa stout, up to 100 μ wide at base and 60 μ wide near apex; excurrent into a short or long spinulose arista, cross section showing 2–3 rows of guides and a convex dorsal sterid band with or without a few ventral sterids; leaf margins revolute to a variable height up to about $\frac{2}{3}$ the leaf length, usually widely recurved at the base and becoming more narrowly so above, upper margins plain, bistratose and doubly serrate with rather small teeth. Upper median cells quadrate to sublinear or irregular, often one shape will predominate over others, oblong seems to be the commonest form, 4–8 × 6–15 μ, papillose on both sides with a single papilla in or near the center of each cell, all cell walls thick, unistratose except the outer marginal rows and sometimes at the apex where the margin merges with the costa; marginal cells usually narrower and thicker-walled, cells of teeth slightly larger. Basal cells wider, quadrate to oblong, mostly 10–14 μ wide,

occasionally some leaves show a few sublinear cells; basal marginal cells becoming shorter, quadrate to transversely elongated.

Dioicous. Perigonium terminal, becoming lateral or axillary by innovation and subtended by 1–4 branches, rather small, ovoid and bud-like; inner perigonial leaves with broad clasping bases, abruptly narrowed to a very long slender, linear apex, costa narrow, long excurrent to a straight or flexuous awn.

Perichaetium terminal becoming lateral or axillary by innovation, subtended by 1–3 branches, rather small, perichaetial leaves narrower than stem leaves, base ovate, tapering to a linear apex, costa narrow, percurrent or excurrent to a long straight or flexuous awn which reaches the base of the capsule, upper cells linear, some papillose at both ends.

Fruit rare, seta short, curved to sigmoid, 1 cm. long or less, usually about as long as the capsule, brownish-yellow or straw-colored. Capsules nearly globose, 3–4 mm. in diameter, irregularly wrinkled when dry, reddish-brown, neck region small, usually not differentiated, mouth very small, lid low convex, annulus lacking. Exothecial cells thin and transparent, irregularly quadrate to hexagonal, below mouth 6–8 rows becoming smaller, thicker-walled, darker colored, and transversely elongated; also becoming smaller and darker in the neck region, with numerous sunken stomata. Spores ovoid-reniform, about 17–27 μ, slightly roughened with low convex wart-like papillae.

Habitat: on dry or damp soil, among rocks and in ledges, in open places or in densely shaded forests, sometimes epiphytic on trees. 2000–3700 M. (about 3000–11500 feet). Mexico, Central America, Colombia to Peru.

Specimens examined: Mexico: Pringle, C. G. Plantae Mexicanae. 10507, cold ledges; 10428, 15224, Cima, 10,000 feet, Federal District; 10442. Sierra de las Cruces, 9,500 feet, State of Mexico. Hahn, 1. On lava rock, Mexico. Arsène, Bro. G., Plants of Mexico 4783. Cerro Azul, Vicinity of Puebla, State of Puebla, 2,300 M.; 4976. l. loc.; 5100. Cerro San Miguel, Vicinity of Morelia, State of Michoacán, 2,200 M.; 7501. l. loc.; 7563 and 7565. Campanario, 2,200 M. l. loc.; Orcutt, C. R. Mosses of Mexico. 6780, 6781. Mineral del Chico, State of Hidalgo. Knoblock, Irving 10,007. Mojarachic, Rayon District, Chihuahua. Wagner, Am Wege nach Guadelupezcalva auf Fels blocker im Schnee. 1897 [as *Bartramia* (*Anacolia*) *subintertexta* C. M. ined.]; Ehrenberg, Cerro de los Navajeo; Bourgeau 1368; Barnes & Land, Pl. Mexicanae 412. Boundary between States of Morelia and Mexico, La Cima, 9900 feet, on shaded lava blocks. 1908; Diguet 5, Sierra de Tlalpujahua, 2000 m.; C. A. Purpus, Popocatepetl (as *A. mexicana* Broth. ined.); Herb. de Thümen, Orizaba. Guatemala: Standley & Steyermark Pl. of Guatemala. 34764. Terrestrial on bank of steep rocky slopes, 2,500–3,700 M.; Volcán Santo Tomas; 34765. Terrestrial on rock bank of steep slopes, l. loc.; 50231. Terrestrial, Pinus-Juniperus woodland near Tojquita, summit of Sierra de los Cuchumatanes, 3,700 M.; 46932. Volcán Santa Clara, 2,100–3,000 M.; 81090. Alpine meadow, Region of Chemal, l. loc. 3,000 M.; 84180. Damp bank in Pinus-Cupressus forest, Region of los Alonzo, mountains above San Juan Ostuncalco, 2,700–2,800 M.; 81691. On limestone in Juniperus forest, Sierra de los Chuchumatanes, 3,300 M.; 83088 a. In shade of dense Juniperus forest, l. loc.; 81677. On rock in Juniperus forest, l. loc.; 35896. Epiphytic on tree trunk, on top of ridge. 3,800–4,000 M. Colombia: Mortiz, 1845. Silla de Caracas. Peru: A. Weberbauer 173. an der Lima-Oroya Bahn, Bergstock im Hintergrunde des Thales Huillacachi südweste von Matucana, an Felsen über 3,000 m. Dec. 28, 1901.

The outstanding characteristics of this species are the unistratose leaf lamina, the strong centrally located papillae of the leaf cells, the oblong to

quadrate inner basal cells and the short curved seta. The most variable characters appears to be in the leaf shape. Typical forms have a rather broad base, up to 0.8 mm. wide at the base, the upper portion rather suddenly tapered to a long lanceolate apex terminating in a stout, serrate awn which may be short or rather long, occasionally extending as much as 1 mm. beyond its junction with the lamina. In most collections the leaf length falls within the usual limits of 2–3.5 mm. but in some the base is narrower giving the leaf a more lanceolate outline. There may be considerable variation in shape in the same tuft, and often on the same stem. These variations are shown in the figures and are taken from Pringle's number 10442 and Orcutt's 6781. While the broader-leaved plants appear to be more like the type, most of the plants examined have narrower leaves. Considerable variation in the shapes of the upper leaf cells was observed. A mixture of shapes in the upper lamina is a characteristic of the genus although one particular shape may predominate. Thus, the cells may be predominately oblong, others may be predominately sublinear and still others shortly rectangular, but in all cases with other shapes present.

Weberbauer's specimen no. 173 from Peru has an unusual habit. The main stems are more or less prostrate with numerous short and closely disposed branches on the upper side, and when dry the tips are strongly curved and hooked giving the plant a most unusual appearance. The leaves are smaller than usual and very dense.

Bartramia (*Anacolia*) *subintertexta* C. M. inedit. is a small form having short curved branches with small dense leaves closely imbricated when dry. The leaves range from 1.5–2.5 mm. long and show considerable variation in form when taken from different points on the stem or from different plants. Some are the shape typical of the leaves of the average forms of *A. intertexta* in being dilated and ovate at the base and rather suddenly tapering to a lanceolate-subulate upper portion but others are narrowly lanceolate and more evenly tapering upward with the base little or not at all dilated. Some larger specimens of *A. intertexta* frequently show similar variations in leaf form so that the present plant has only its small size as a distinctive feature which is scarcely enough to warrant separation.

Anacolia mexicana Broth (in herb.) is in no way sufficiently different from the general range of the species to warrant separation.

Brotherus (Engler and Prantl, Ed. 2, p. 499, 1924) cites this plant as *Anacolia setifolia* (Hook.) Jaeg. on the basis of priority and Mitten's statement that he had found it to be identical with *A. intertexta*. I have seen the type of Hooker's *Gymnostomum setifolium* together with other simliar specimens in the Mitten herbarium and they all belong to *Leiomela*. The latter should be cited as *Leiomela setifolia* (Hook.) n. comb.

a. Var. **latifolia** var. nov., figs. 25–32.

Plantae caespitosae; caulis 4–5 cm. altis, erectis vel ascendentibus; fasciculus centralis magnus, $\frac{1}{3}$–$\frac{1}{4}$ diameter caulis. Folia 2–2.5 mm. longa, 0.6–0.8 mm. lata in basi, sicca dense imbricata, aliquanto crispata, humida patentia, ovato-lanceolata, breviter acuminata, concava, latiora in parte superiore quam aliae species, haud abrupte angustata; costa brevis excurrens; cellulis superioribus saepe breviter oblongis vel quadratis, 6–9 μ latis, incrassatis; papillis mediis; cellulis basilaribus quadratis vel oblongis, 8–12 μ latis.

Plants in loose tufts, yellowish-green above, darker below; stems up to 5 cm. long, erect or with ascending branches from a more or less prostrate main stem, *central strand larger* than in *A. intertexta*, $\frac{1}{3}$–$\frac{1}{4}$ total stem diameter. Leaves 2–2.5 mm. long, 0.6–0.8 mm. wide at base, rather closely disposed, when dry slightly crisped, spreading above; when moist spreading at about a 45° angle, *ovate-lanceolate*, not abruptly narrowed from the base, shortly acuminate, upper portion broader than any other species; costa shortly excurrent to a stout moderately spinulose point (sometimes forming a short awn), very concave to near the base of the apex, margins revolute $\frac{1}{2}$ length of leaf or up to a point just short of the apex, closely double serrate with moderately-sized teeth; upper lamina single stratose, except for the bistratose marginal rows of cells, upper cells mostly shortly rectangular, quadrate or slightly irregular, 6–9 μ wide, moderately thick-walled, papillae large, central. Inner basal cells shortly rectangular to quadrate, wider, 8–12 μ wide; basal marginal cells predominately quadrate. Type sterile, in Chicago Natural History Museum.

On limestone. Guatemala, Dept. of Huetuetenango: El Mirador, at summit of road leading from Huetuetenango to Sierra de los Cuchumatanes, alt. about 3,340 M. Standley, Field Mus. of Nat. Hist. Exped. Pl. Guatemala 81852.

This plant is quite distinctive both in general appearance and in the shape of the leaves. In general the stems have a more compact and somewhat swollen appearance when dry due to the broader leaves without long narrow points and as a result it does not have the somewhat plumose appearance of other species. The outline of the leaves recalls that of certain species of *Bryum*. The upper lamina is unistratose with the exception of cells here and there bistratose. The shorter cells are also distinctive.

b. Var. ARISTIFOLIA Thér. Smithsonian Misc. Coll. 78 (2): 18. 1926.

Differs from the species in that some of the upper leaves have very long excurrent costae some of which extend 1.5 mm. beyond the leaf lamina.

Arsène, Bro. G. Pl. Mexico. 4873, 5076 Cerro San Miguel, 2200 M., Vicinity of Morelia, State of Michoacán, Mexico.

According to the original description "this variety differs from the type in that the leaves are narrower at the base, more gradually and more finely acuminate, less strongly revolute and for a shorter distance, and less sulcate.—the median cells are narrower (6–7 μ) with less thickened walls." Several specimens of Arsène's nos. 4873 and 5076 were available and in both there are some stems bearing leaves that fit the above description but

also mixed with them are stems having leaves very broad at the base and variable with respect to the other characters. Most of the plants have the unusually long excurrent costa which appears to be the only constant character. *Anacolia mexicana* Broth, here referred back to the species, has a rather long excurrent costa and broad leaf base somewhat intermediate between the species and this variety.

5. **Anacolia abyssinica** (C.M.) comb. nov., figs. 50–55.
Bartramia abyssinica C.M. Syn. I. 506. 1849.
Glyphocarpa abyssinica Hampe in herb.

Plants loosely tufted, yellowish-green above, reddish-brown below; stems erect or ascending, straight or curved, up to 6 cm. tall, 0.4–0.6 mm. in diameter, central strand large, ¼–⅓ the stem diameter. Leaves dense, when dry appressed and imbricated, little changed; when moist erecto-patent to patent, straight, 3–4 mm. long, 0.7–0.9 mm. wide at the base, ovate-lanceolate to long triangular-lanceolate, lamina unistratose, sometimes bistratose here and there or in short uniseriate lines; base concave with two main folds and 2–4 smaller plicae; costa very stout below, up to 130 μ wide at the base, mostly excurrent to a short or long spinulose arista, prominent at the back, smooth or somewhat toothed above, guides in 1–2 rows with a strong dorsal sterid band, with or without a few sterids ventral (exclusive of the superficial cells); margins narrowly revolute on one or both sides, occasionally becoming plain at the base, moderately double serrate above, entire below. Upper cells oblong to shortly rectangular, rhomboidal or irregular, thick-walled, mostly 4–8 μ wide, papillae large, central; marginal cells not or only slightly larger than those of the main lamina, cells of the teeth about the same size, not very coarse but thicker walled. Inner basal cells oblong to shortly rectangular, 6–10 μ wide, basal marginal cells shortly rectangular to quadrate or transversely elongated.

Dioicous. Perigonium not seen. Perichaetium terminal, inner leaves longer and narrower than the stem leaves, 5–6 mm. long, base less broadened, gradually tapering upward to a linear upper portion, margins finely and distantly serrulate above, costa strong, long excurrent, finely spinulose aristate, basal cells irregularly quadrate to oblong, 4–6-sided, thin-walled and hyaline, upper cells mostly linear; archegonia rather numerous, about 0.75 mm. long, paraphyses numerous. Sporophyte lateral by innovation, sometimes subtended by two branches; seta arcuate to nearly erect, 2.5–3.5 mm. long; capsule globose, strongly rugulose when dry, 2.5–3 mm. in diameter, yellowish-brown, reddish at the mouth and base, mouth small; exothecial cells 30–50 μ wide, 4–6-sided, irregularly oblong, some isodiametric or transversely elongated, thin-walled; lid low convex, reddish-brown; spores reniform, 25–30 μ long, yellowish-brown to dark reddish-brown, beset with low, coarse papillae. Type locality Abyssinia.

Specimens examined: W. Schimper 770, 967 and two without numbers. Abyssinia. Verdoorn, Mus. Sel. et Crit. 130. Africa orient.: Eritrea, in m.d. monte Soiva, in decliv. irriguis, ad rupes siliciosas, 2400 m.

Two plants from Abyssinia are treated as synonyms by Paris (Index bryol. I, 23, 1904). He gives *Anacolia abyssinica* Schimp. with *Bartramia abyssinica* C. M. and (ibed. II, 257) *Glyphocarpus abyssinicus* Jaeg. in herbarium as synonyms. At the close of his description of *Bartramia abyssinica*, C. Müller (l.c.) cites *Glyphocarpa abyssinica* Hampe in herbarium as a synonym of his name.

The original description of *Bartramia abyssinica* C.M. is quite clear and fits the plant very well although some important features are not mentioned. The original description of *Anacolia abyssinica* Schimp. is very short but there is no doubt as to which plant it was intended to apply. However, I find that Schimper's plant differs in no essential character from *Anacolia laevisphaera* (Tayl.) Flowers which has an earlier date of publication.

When first discovered by Schimper the plants were referred to the western Mediterranean species *A. webbii* which at that time was known variously as *Bartramia* (*Glyphocarpa*) *webbii* or *Bartramia granatensis*. Under the latter names several exsiccatae were issued. Those I have seen, including W. Schimperi iter Abyssinicum no. 441 (in part), are all *A. laevisphaera*. Ironically Schimper distributed other specimens (e.g. nos. 770 and 967 and some without numbers) under his newly created genus and species, *Anacolia abyssinica*, which are actually Müller's *Bartramia* (*Anacolia*) *abyssinica*.

Anacolia abyssinica, *A. intertexta* and *A. sinensis* are so much alike that there is little to distinguish them. The specimens of *A. abyssinica* available for study have a much larger central strand than the other two species and it appears to be a constant feature. Several specimens of *A. sinensis* I have seen are much larger plants with larger leaves less serrate at the tip than the other two plants. The wide geographical separation of the three species is significant but the lack of a larger series of the eastern hemisphere members leaves some doubt concerning their range of variation and sporophytes. For the present it is perhaps better to consider them separate species until more is known about them.

6. ANACOLIA SINENSIS BROTH., figs. 56–64. Sitzungsber. Akad. Wiss. Wien. Mat.-Naturw. Kl. Abt. I, 133: 570–71. 1924.

Plants large and loosely tufted, yellowish-green above, reddish-brown below. Stems up to 20 cm. tall, erect or ascending, branches usually distant and more or less spreading, often slightly hooked at the tip when dry, central strand small, $\frac{1}{6}$ the diameter of the stem or less. Leaves dense, when dry appressed and imbricated, the tips often divergent, not greatly changed to somewhat crisped; when moist erecto-patent, to patent, 3–5 mm. long, 0.8–1 mm. wide at the base, ovate-lanceolate to long and narrowly triangular-lanceolate; lamina unistratose; base with two large folds and 2–4 smaller intermediate plicae; costa stout, up to 105 μ wide at the base, percurrent to shortly excurrent, prominent at the back, smooth or slightly toothed above, guides in 1, 2 or partially 3 rows, with a strong dorsal sterid band, with or without a few sterids ventral (exclusive of the superficial cells); margins bistratose near the apex, and here and there below, not extending as far toward the base as in other species, revolute for half the leaf length or more, often widely recurved near the base, moderately serrulate to subentire above, teeth double, often single here and there. Upper cells oblong to linear, 3–8 μ wide, predominantly linear in some leaves, on the average narrower than in other species, papillae large and central. Basal cells

oblong to quadrate, 5–9 μ wide, basal marginal cells shortly rectangular to quadrate or transversely elongated.

Dioicous. Perigonia terminal, rather large, becoming subtended by or lateral by innovation, when present usually abundant, outer leaves much like the stem leaves, inner ones becoming progressively differentiated, the base broadly ovate and clasping, about 1 mm. long, with irregular oblong, hyaline, thin-walled cells, the upper portion suddenly narrowed and more or less squarrose-divergent, linear, straight or strongly flexuose, 3.5–4 mm. long (base not included), margins entire to weakly dentate, costa weak above, often indistinct in the apex; extreme inner leaves often broadly ovate-acute, consisting of base only, the upper portion suppressed; antheridia reddish-brown, numerous, about 0.73 mm. long, paraphyses numerous, linear, exceeding the antheridia. Perichaetia terminal, when present often numerous, inner leaves with the base ovate to oblong, half clasping, the cells oblong, hyaline, and thin-walled, the upper portion more gradually tapering to a linear, straight or flexuose apex, archegonia few, about 0.75 mm. long, paraphysese few. Sporophyte terminal, soon becoming lateral by innovation, (occasionally terminal and axillary between two innovations); seta 2–4 mm. long, curved or arcuate; capsule subglobose, 2–2.5 mm. in diameter, yellowish-brown, strongly rugulose when dry, mouth small, exothecial cells 4–7-angles, mostly irregularly oblong-hexagonal, some more or less isodiametric, thin-walled, mostly 33–56 μ wide; lid not seen. Spores reniform, 16–20 μ long, yellowish to dark yellowish-brown with low, moderately coarse papillae. Type locality China: Setschwan. Type seen.

Specimens examined: Handel-Mazzetti, iter sinensis, 1914–1918. 2189. China (prov. Setschwan austro-occid.): in regionis temperatae inter oppidum Yenyüen et flumen Yalung (27° 30′) bambusetis declivitatis septentr. montis Dadjin, ad rupes arenaceas, alt. s. m. ca. 3200–3400 m. Leg. 11. V. 1914. (Type with fruit). Under the label Krypt. exsicc. 2882. the same data are given with the following note "m.m. speciem. originale." Prov. Yünnan bor.-occid. No. 3469. In regionis temperatae prope urbem Lidjiang ("Likiang") rupibus sub jugo Duinaoko ducente. Substr. calceo, alt. s.m.ca. 3000–3100 m. Leg. 4. VI. 1914. No. 4285. In montis Yülung-schan prope urbem Lidjiang ("Likiang") regionis frigide temperatae rupibus ad rivulum supra pratum Ndwolo. Substr. schisto argilloso; alt. s.m. ca. 2700 m. Leg. 2–. VII. 1914. No. 6767. In montis Yao-schan prope vicum Ganhaidse ad urbem Lidjiang ("Likiang") regione frigide temperatae ad rupes. Substr. calceo; alt. s.m. ca. 3750 m. Leg. 13. VI. 1915. 6392. China: Prov. Yünnan: In montis Dji-schan ad boreo-orientem urbis Dali (Talifu) regione temperatura, ad rupes, Substr. diabasico, alt. s.m. ca. 3050–3350 M. Leg. 21. V. 1915.

The specimens I have seen are large and stout, about the size of larger forms of *A. laevisphera* but stouter in thickness of the shoots. The branches are more distant and more widely spreading. It is closely related to *A. intertexta* but is stouter and on the whole the leaves are larger, the margins less serrate and the upper cells narrower. In some stems of *A. sinensis* the leaves are much longer and narrower than those illustrated. It is also much like *A. abyssinica* differing in the larger size and the smaller central strand of the stem.

7. ANACOLIA MENZIESII (Turn.), figs. 66–76. Paris, Index Bryol. (Ed. 1) 27. 1894.

Bartramia menziesii Turn. Koen. & Sims, Ann. Bot. 1: 525. pl. 2, f. 1. 1805;

Brid. Bryol. Univ. 2: 48. 1827; L & J. Manual. 204. 1884. Sulliv. Icones Musc. Suppl. 39. t. 26. 1874.

Glyphocarpus menziesii (Turn.) Jaeg. Jahresb. St. Gall. naturwiss. Gesel. 63, 1873–74. Ad. I. 525. 1873–74.

Anacolia menziesii var. *crispa* Ren. in herb.

A. braunii Kindb. Can. Mosses (no number; nomen nudum).

Philonotis leiophylla Kindb. (in part). nomen nudum.

Plants in dense tufts, variable in color, yellowish-green, or dark green above, reddish-brown to blackish below, usually with a dense tomentum of reddish-brown rhizoids extending high up on the stems but sometimes with only a few at the base. Stems branched, erect or ascending from prostrate main stems, 8-angled, papillose, 3–5 cm. tall, mostly yellowish green, often darker brownish below; leaves 8-ranked, appressed and imbricated when dry, erecto-patent to subspreading when moist, occasionally recurved and falcate, mostly 2.5–3.5 mm. long, 0.4–0.7 mm. wide at base, variable, in some plants shorter, in others long, *narrowly lanceolate from an ovate base,* concave below and deeply channelled above, base with a strong fold on either side, sometimes with smaller plicae between, margin revolute to widely recurved $\frac{1}{2}$–$\frac{7}{8}$ leaf length, marginal cells bistratose or partially so above, moderately doubly serrate above, sometimes merely dentate; costa typically *stout and percurrent to shortly excurrent,* forms with long excurrent costae are common, in cross section showing 1–2 rows of hypodermal guides and a dorsal sterid strand (occasionally a few small sterids stand ventral), dorsal and ventral superficial cells small, rather thick-walled; upper lamina variably bistratose, sometimes with entire upper area two-layered, often bistratose in lines or merely a few cells here and there, occasionally completely unistratose throughout; upper cells variable, typically shortly rectangular to oblong, often with a few linear cells here and there, or in lines; in some forms quadrate to shortly oblong; mostly 7–10 μ wide, linear cells narrower, *smooth or with low rounded papillae on the ends on the ventral surface,* occasionally strongly papillose; *inner basal cells quadrate to shortly rectangular,* 8–12 μ wide, somewhat wider and shorter on the basal margins.

Dioicous. Perigonia terminal, becoming lateral by innovation, somewhat gemmiform, perigonial leaves lanceolate-subulate from a broadly ovate or oblong, concave and subsheathing, colored base; perichaetium terminal becoming lateral by innovation, leaves much like those of the stem, somewhat narrower. Seta erect or curved, 5–12 mm. long, yellowish to reddish-brown; capsules globose to shortly ovoid, 2.2–2.8 mm. long, reddish-brown when mature, neck usually lacking or sometimes very short, leptodermous, rugulose when dry, fragile and often split, mouth small, exothecial cells quadrate to oblong and many-sided, thin-walled, 40–66 μ wide, small, thicker-walled and more highly colored below the mouth; peristome mostly lacking, when present variously developed, occasionally as a low, thin membrane within the mouth, sometimes with a few joints but more often as short distinct lanceolate teeth varying up to 12 joints high arising well within the mouth, pale yellowish to reddish-brown, often strongly jointed, smooth, very fragile and often broken; lid variously conic, obtuse. Spores globose to reniform with large low warts, 28–32 μ. Type locality Northwest Territory (probably Oregon).

On rocks, in crevices and on soil, usually in shade. Alaska southward through British Columbia to southern California, eastward to northern Idaho and Montana, Yellowstone National Park in Wyoming.

Specimens examined: British Columbia: Macoun 100. Damp rocks, Craigflower Road, Vancouver Island; Can. Musci 151 (as *Philonotis leiophylla* Kindb.); Fl. Canada 247 and 2112. Vancouver Island; Several other specimens without number and data other than Vancouver Island. J. Röll 51. Victoria, Vancouver Island. Washington: J. Röll 613. Cascaden, Easton; N. L. Gardner 148. Decemtion Pass. G. N. Jones 2948. Steep vertical cliff, Deadman Lake, Adams County; 2985. Rocky hillside, Goodnoe Hills, Klickitat County. Oregon: Menzies, Northwest America (Type ? in Mitten Herbarium); J. Röll. 1045. Mt. Hood; Rau, Amer. Mosses 23. Portland; Holzinger. Musc. Acro. Bor. Amer. 165. On basaltic walls, Willamette river gorge, 250 feet, near Oregon City. Idaho: J. Röll 1180. Coeur d'Alene. California: Verdoorn: Musc. Sel. et Crit. 104, California, Placer Co., Canyon Creek, Dutch Flat; Sull. et Lesq.. Musci Bor. Amer. 259. (Ed II) (as *Bartramia*); Howe, M. A. Musci Calif. 48, on rocks in woods, Shasta springs (in part); 762 and 772. Doolan's Canyon, Ukiah, Mendecino County; A. A. Beetle Pl. Calif. 3852. Putah Creek west of Winters, Solano County. F. A. MacFadden 9656. Dutch Flat, Placer County; 17437. On earth at base of cliff, Yosemite Nat. Park; Bolander, Rupi ombrose, California inferiore; 2033 and numerous other specimens without numbers or other data; L. J. Newton, Nordhoff, Ventura County; Kleeberger, Trinity County; Bennett 295; R. S. Gray 541. Oakland: Ralf Lyon 14. Near Auburn; W. C. Blasdale, Redwood Canyon, Marin Co.

Like other species of the genus this plant shows considerable variation in stature and in the shape and structure of the leaves. Typically it is bright yellowish-green above, and brownish-green below with a dense felt of bright ferruginous rhizoids emerging from among the leaves. In contrast, it may be dull green throughout, sometimes various shades of green above and blackish or dark brownish below. The rhizoids may be few and the typical felt-like growth lacking. The leaves are extremely variable in outline and size. Plants growing on very dry rocks in both woods and open sagebrush land show short broad leaves, 1.5–2 mm. long and have been designated as *forma brevifolia*. Forms with large leaves, 3.5–5 mm. long, narrowly linear-aristate from a rather narrow base are called *forma grandifolia*. Intergraduations among these forms are common.

The concept of this species has been greatly influenced by Sullivant's illustration in his Icones Muscorum Supplement, plate 26, and by several standard exsiccati including Howe's Musci of California 28, Sull. and Lesq. Musci Bor. Amer. (Ed II). 259, Renauld and Cardot's Musci Amer. Sept. 53 and 220. From these sources one gains the impression that the typical form of the plant has rather short broad leaves with a stout, shortly excurrent costa as shown in Fig. 68. The type was not available for study but a specimen in the Mitten herbarium labeled *Bartramia menziesii*, N.W. Amer., Menzies is possibly a portion of the original material. It has much longer and proportionately narrower leaves with the costa excurrent to a long slender arista as shown in Fig. 69. This gives a broader concept of the species. *Anacolia aristifolia* was erected for larger forms with exceedingly

long slender tips on the leaves. It is here reduced to *forma grandifolia*. A great many specimens were available for study and among them are numerous intermediate types that filled in the gaps which formerly seemed to exist between several forms.

Variations in the species are probably traceable to habitat conditions although the data on the packets are often too brief or lacking to draw satisfactory conclusions. It was noted that most of the plants collected in the southern half of California have leaves of the shorter form while the majority of those from the northern part of the range are taller and more robust with long slenderly aristate leaves. However, the plant showing the shortest leaves (forma *brevifolia*) was collected in Washington. From the distribution and such data as are available it appears that the smaller, short leaved forms grow in drier habitats and the larger forms in moist or humid situations.

6[1]. Forma **brevifolia**, forma nov., fig. 77. Plantae humiles caespitosae, obscure coloratae, fusco-flavescentes vel fusco-nigrescentes subter, caules 2–4 cm. altis, folia sicca imbricata, aliquanto crispata, humida patentia, rigida, ovato-lanceolata vel anguste lanceolata, in basi latissima, 1.5–2 mm. longa, 0.55–0.65 mm. lata; costa percurrente vel excurrente, marginibus hebeter dentatis. Cellulis superioribus quadratis vel breviter oblongis; cellulis basilaribus similaribus. Caetera ignota.

Plants in short dense tufts, darker in color, brownish-yellow to blackish-brown below, 2–4 cm. high, rhizoids few and inconspicuous, stems erect or curved, branches parallel, leaves closely imbricated when dry; spreading stiffly when moist; shorter and broader in proportion than in the species, ovate-lanceolate or narrowly lanceolate from a very broad base, 1.5–2 mm. long. 0.55–0.65 mm. wide at base; upper lamina unistratose or bistratose only here and there in lines; upper cells shorter, quadrate to shortly oblong, basal cells about the same; margin merely bluntly dentate, costa percurrent to excurrent. Sterile. Type; Jones 2987. In Herbarium of S. Flowers. On dry basalt rocks in shade, Washington. Chapman Creek, Klickitat County.

This is the least typical in appearance of any form. Some of the dry stems appear very slender, the leaves so closely appressed and imbricated as to give them a mouse-tail appearance. The short leaves with very short cells are distinctive. It appears to grow in much drier places than other forms.

Specimens examined: Jones 2986, and 2987. On steep north cliff (basalt), 221 feet elev., Chapman Creek, Klickitat Co., Washington.

6[2]. FORMA GRANDIFOLIA Flowers, in Grout, Moss Flora N. Amer. II, 156. 1935.

Anacolia aristifolia Flowers, fig. 78. l.c. p. 156.

Plants in robust caespitose tufts, 5–12 cm. high; stems densely reddish tomentose below, branched; leaves appressed and imbricated with the tips often somewhat divergent and twisted when dry; open to widely recurved when moist, *lanceolate aristate, 3.5–5* mm. long, *0.7–0.9 mm. wide at the base;* costa stout, excurrent into a long, spinulose arista, often extending 1–1.5 mm. beyond the lamina. Capsule as in the species, spores 26–30 μ.

On shaded rocks, British Columbia, Washington, Oregon, northern Idaho and northwestern Montana.

Specimens examined: British Columbia: Macoun Can. Musci 17. on rocks; 118. Colquintz river; 195. on rocks, Biological Station, Apartine Bay. Several other specimens without numbers, two labelled Vancouver Island. Washington: J. Röll 612 and 614. Cascaden, Easton. Foster, several specimens without numbers. Oregon: Howell Musci Oregonensis. Rooster Rock. Idaho: Leiberg 122, northern Idaho. Sandberg. 74. 1892. Montana: R. S. Williams N. Amer. Mosses 221. on rock wall, Columbia Falls.

Larger than the species with leaves larger and more constantly long excurrent. In vegetative characters it cannot be distinguished from large forms of var. *baueri*, but it has the globose capsules like the species.

6a. Var. BAUERI (Hampe) Paris, figs. 79–81. Index Bryol. (Ed. I) 27. 1894.

Glyphocarpa baueri Hampe, Linn. 30: 457. 1859.

Bartramia menziesii var. *Baueri* R. & C. Rev. Bryol. 19: 94. 1892.

Anacolia menziesii var. *longicarpum* Ren. nom. nudum; in herb. no. 61.

Much like the species in vegetative characters but the leaves in most of the specimens observed are somewhat longer and the costa mostly shortly excurrent but in general they are variable in the same respects described in the species. *Seta 7–17 mm. long, straight or flexuose, capsules oblong to shortly cylindrical, often with a short neck, 2.4–3 mm. long including lid,* yellowish or reddish-brown; peristome lacking or composed of 16 irregular short teeth arising half their length below the mouth, lanceolate or shorter and blunt; lid conic-obtuse; spores globose to reniform, papillose, mostly 18–22 μ, occasionally up to 26 μ. Type locality California. On rocks and in crevices of cliffs in shaded places, British Columbia to southern California; northern Idaho.

Collections examined: British Columbia: Macoun Can. Musci 151; Idaho; G. N. Jones 814. Common on moist basaltic ledges, Big Canyon Creek. California: Holzinger, Musc. Aero. Bor. Amer. 602 on rocky hillsides, not fruiting freely but occasionally patches show many capsules. Orroyo Seco, Switzerland, San Gabriel Mts.; Howe, Musci California 48b; Howe. 747. Doolan's Creek, Ukiah, Mendecino County and two others without numbers; Ren. & Card. Musc. Amer. Sept. 220, Sull. & Lesq. Musci Bor. Amer. (Ed. 2) 260; Grout, Musci Perfecti 305; N. A. Musci Perf. 320. On shaded rock ledge along creek, alt. about 2000 feet, North Fork; Bolander 15. ad rupes, Mission Dolores, prope San Francisco; Leiberg 5494. On rocks near Bidwell Bar, California; F. A. MacFadden 9639. Cliffs, Bear River, Liberty Hill Road, Dutch Flat, Placer Co. and Stow Canyon off La Tuna Canyon, Verdungo Hills, Los Angeles Co., California; Beetle A. A., Pl. Calif. 3845, Solano Co., Putah Creek Canyon west of Winters; Kingman, C. C., Mosses So. California. 695. Rubio Canyon, Pasadena.

The capsule and spores are the only reliable characters for distinguishing this variety. The vegetative structures show nothing constant that can be used in segregating it from the species. It is more common in the southern half of California and becomes less frequent northward. It is apparently favored by a drier habitat.

EXCLUDED SPECIES

ANACOLIA DIDYMOCARPA (Schimp) Paris, Suppl. Index. p. 8. 1900 is a *Bartramia* of the section Vaginella. It was originally named *Bartramia*

didymocarpa Schimp. in herb. C. Müller cited it as *Bart.* (*Anacolia*) *didymocarpa* Schimp. and gave a description in Nuovo. Gior. bot. ital., 45, 1897. Mandon coll. No. 1669, Andes mountains of Bolivia.

ANACOLIA AURICOLOR Dusén, Dusén n. 600. Patagonia occ. is *Breutelia auricolor* (Dusén) n. comb.

ANACOLIA SETIFOLIA (Hook.) Jaeg. belongs in *Leiomela* as *L. setifolia* (Hook.) n. comb.

Acknowledgments. I am especially indebted to Mr. E. B. Bartram whose collections formed the nucleus of this study and to Dr. T. C. Frye who urged me onward in this undertaking. I wish to acknowledge the kindness of the following people for making collections available for study and for bibliographical assistance: Drs. W. C. Steere, University of Michigan, D. P. Rogers, New York Botanical Gardens, Francis Drouet, Chicago Natural History Museum, Winona H. Welch, DePauw University, Hans Buch, University of Helsinki, Mm. V. Allorge, Museum National D'histoire Naturelle, Paris, William Wright Smith, Royal Botanic Garden, Edinburgh and the late Drs. William R. Maxon, U. S. National Herbarium and David H. Linder, Farlow Cryptogamic Herbarium, Harvard University.

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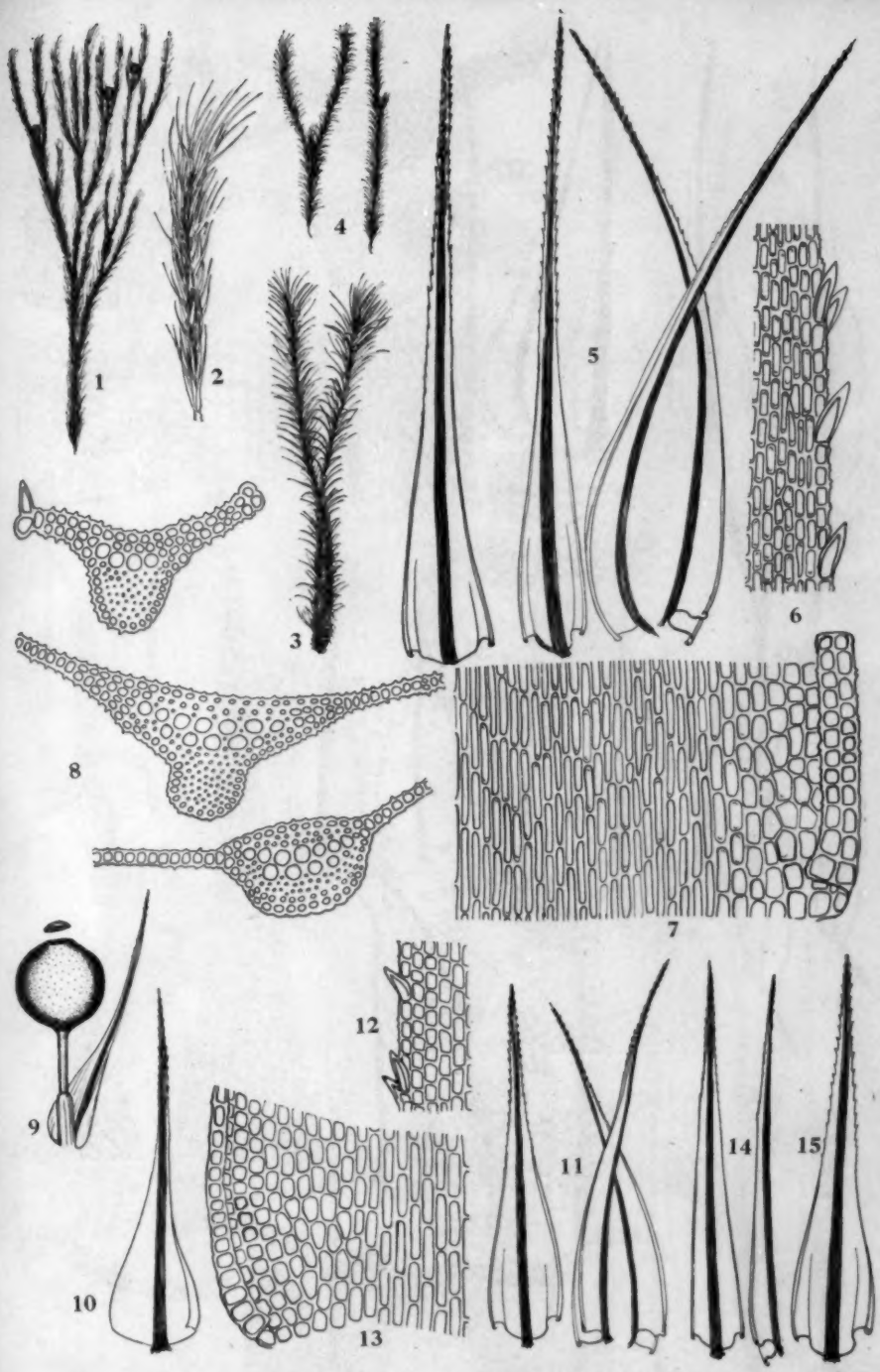
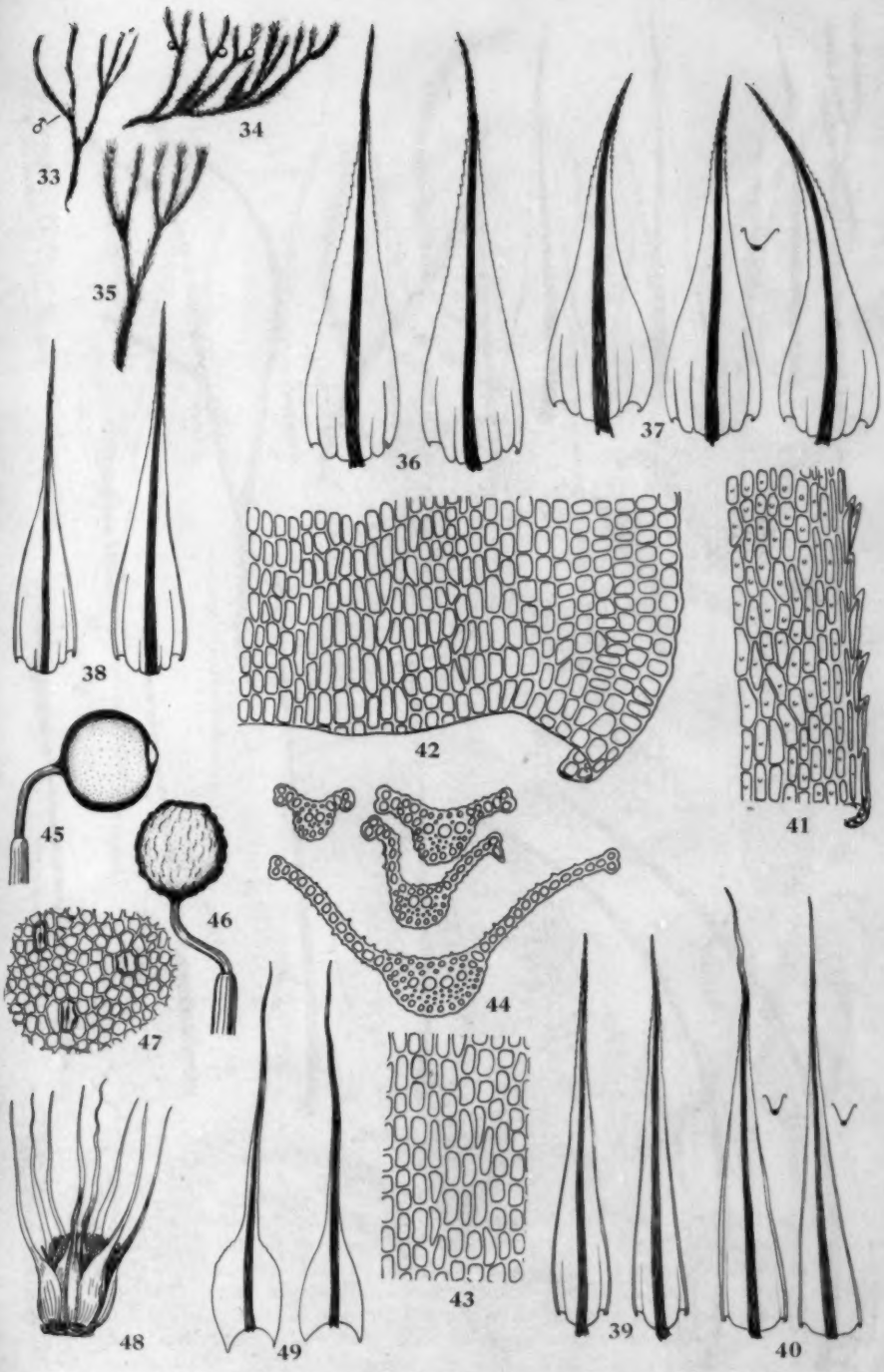


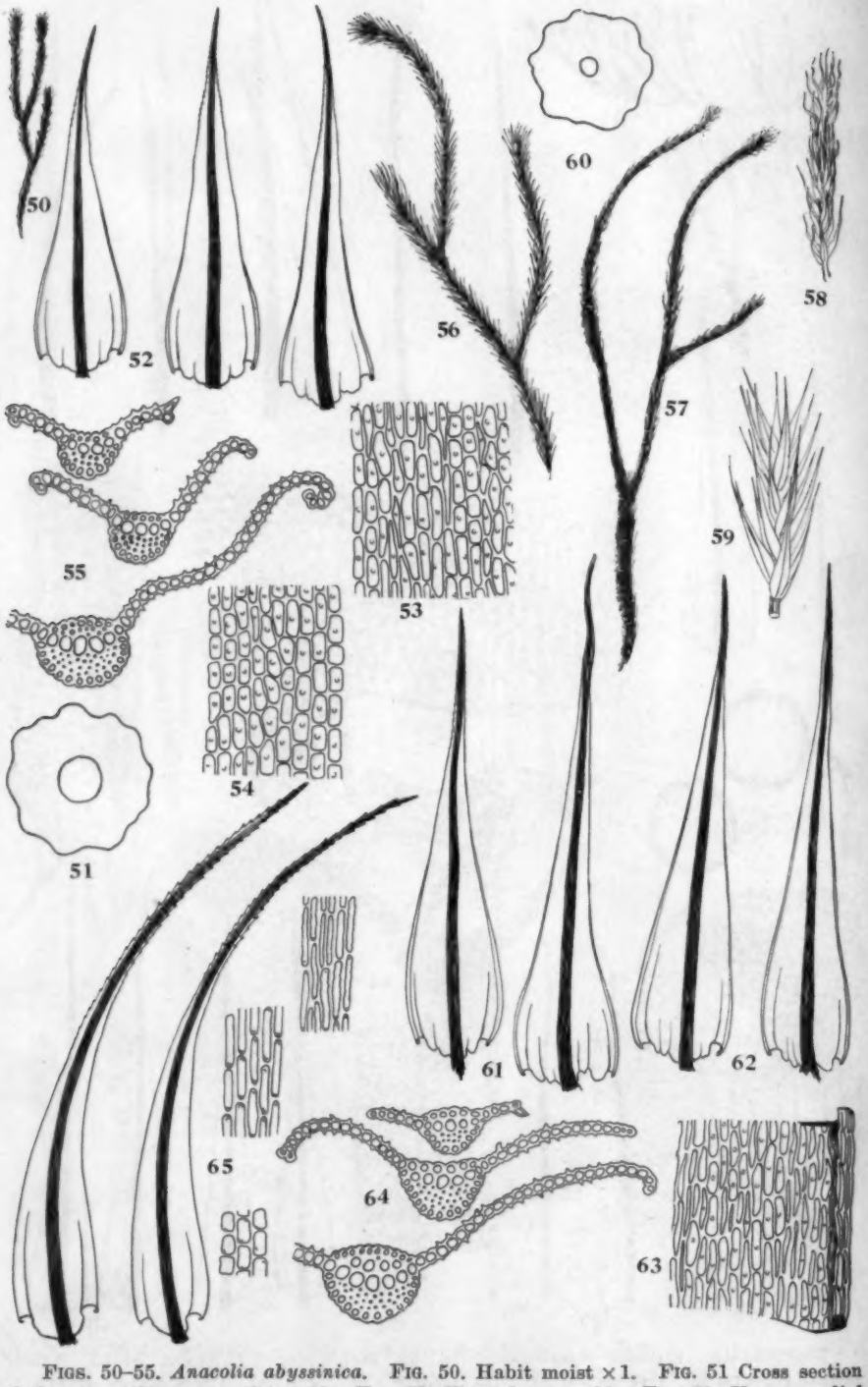
FIGS. 1–15. *Anacolia laevisphaera*. FIG. 1. Habit dry × 1. FIG. 2. Same × 4. FIG. 3. Habit moist × 1 (Herrera 1464a, Peru). FIG. 4. Same (Arsène, Pl. Mexico 7,963). FIG. 5. Four leaves × 30 (Herrera 1,464a). FIG. 6. Upper medial and marginal cells × 300. FIG. 7. Basal medial and marginal cells × 300. FIG. 8. Three cross sections of the costa and lamina at different levels × 300. FIG. 9. Sporophyte moist × 10. FIG. 10. Inner perichaetial leaf × 30. FIG. 11. Three leaves of a small form × 30 (Arsene 18,771, New Mexico). FIG. 12. Upper medial cells of same × 300. FIG. 13. Basal medial and marginal cells of same × 300. FIG. 14. Two leaves of small form × 30 (Hosseus 330, Argentina, Cordoba). FIG. 15. Single leaf of small form × 30 (Hosseus 318, Cordoba.). See also fig. 65.

FIGS. 16–24. *Anacolia webbii*. FIG. 16. Habit dry $\times$ 1. FIG. 17. Habit moist $\times$ 1. FIG. 18. Two leaves $\times$ 30 (Trotter, Corsica). FIG. 19. Two leaves $\times$ 300 (Richards, Spain). FIG. 20. Upper medial and marginal cells $\times$ 300. FIG. 21. Basal medial and marginal cells $\times$ 300. FIG. 22. Cross sections of the costa and lamina at different levels $\times$ 300. FIG. 23. Upper medial cells $\times$ 300. FIG. 24. Basal medial cells $\times$ 300 (Bourgeau 1,586, Canary Islands).

FIGS. 25–32. *Anacolia intertexta* var. *latifolia*. FIG. 25. Habit dry and moist $\times$ 1. FIG. 26. Habit moist $\times$ 5. FIGS. 27–28. Five leaves and a section $\times$ 30. FIG. 29. Two leaf apices $\times$ 300. FIG. 30. Upper medial and marginal cells $\times$ 300. FIG. 31. Basal medial and marginal cells $\times$ 300. FIG. 32. Two cross sections of a leaf $\times$ 300.



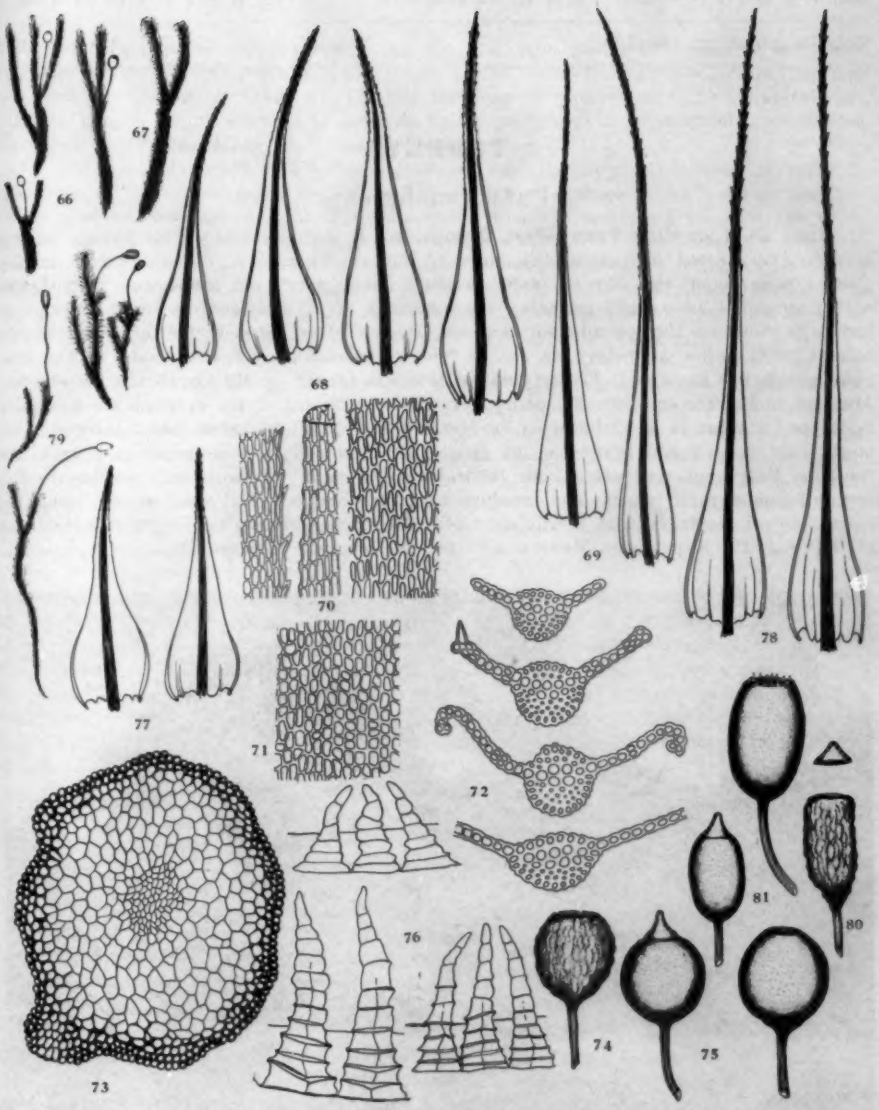
FIGS. 33–49. *Anacolia intertexta*. FIG. 33. Habit dry ×1. FIGS. 34–35. Habits moist ×1. FIG. 36. Two leaves of typical form ×30. FIG. 37. Three leaves of broad-leaved form ×30 (Pringle 10,442, Mexico). FIG. 38. Two leaves of slender form ×30 (also Pringle 10,442). FIGS. 39–40. Four leaves of narrow-leaved form ×30 (Orcutt 6,781, Mexico). FIG. 41. Upper medial and marginal leaf cells of typical form ×300. FIG. 42. Basal medial and marginal cells of same ×300. FIG. 43. Upper medial leaf cells of the shorter and broader type ×300. FIG. 44. Cross sections of the costa and lamina at different levels ×300. FIG. 45. Sporophyte moist ×20. FIG. 46. Sporophyte dry ×20. FIG. 47. Exothecial cells of the neck region showing stomata ×300. FIG. 48. Perigonium ×15. FIG. 49. Two perigonial leaves ×30.



FIGS. 50–55. *Anacolia abyssinica.* FIG. 50. Habit moist × 1. FIG. 51 Cross section of the stem (diagrammatic) × 30. FIG. 52. Three leaves × 30. FIG. 53. Upper medial leaf cells × 300. FIG. 54. Basal medial leaf cells × 300. FIG. 55. Cross sections of the costa and lamina at different levels × 300.

FIGS. 56–64. *Anacolia sinensis.* FIG. 56. Habit moist × 1. FIG. 57. Habit dry × 1. FIG. 58. Portion of the stem tip dry × 5. FIG. 59. Same moist × 5. FIG. 60. Cross section of the stem showing large central strand (diagrammatic) × 30. FIGS. 61–62. Four leaves × 30. FIG. 63. Upper medial and marginal leaf cells × 300. FIG. 64. Cross sections of the costa and lamina at different levels × 300.

FIG. 65. *Anacolia laevisphaera.* Two leaves with upper, middle and basal leaf cells (Diehl 2,549, Peru).



FIGS. 66–76. *Anacolia menziesii*. Three habit sketches of plants from different habitats × 1. FIG. 67. Habit of form with falcate leaves × 1. FIG. 68. Four leaves of typical short, broad type × 30. FIG. 69. Two leaves of the longer, narrow type × 30 (from Menzies' specimen in the Mitten Herbarium which is probably a portion of the original material). FIG. 70. Three sketches of the upper medial and marginal leaf cells × 300. FIG. 71. Basal medial leaf cells × 300. FIG. 72. Cross sections of the costa and lamina at different levels × 300. FIG. 74. Capsule dry × 15. FIG. 75. Two moist capsules × 15. FIG. 76. Three sketches of the peristome teeth showing different degrees of development × 300.

FIG. 77. *Anacolia menziesii* forma *brevifolia*, two leaves × 30.

FIGS. 78. *Anacolia menziesii* forma *grandifolia*, two leaves × 30.

FIGS. 79–81. *Anacolia menziesii* var. *baueri*. FIG. 79. Three habit sketches × 1. FIG. 80. Capsule dry × 15. FIG. 81. Two moist capsules × 15

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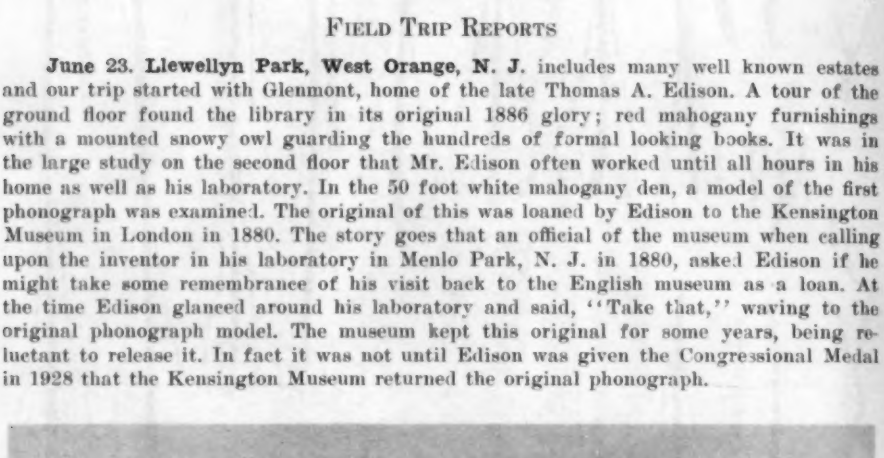
TORREYA

FIELD TRIP REPORTS

June 23. Llewellyn Park, West Orange, N. J. includes many well known estates and our trip started with Glenmont, home of the late Thomas A. Edison. A tour of the ground floor found the library in its original 1886 glory; red mahogany furnishings with a mounted snowy owl guarding the hundreds of formal looking books. It was in the large study on the second floor that Mr. Edison often worked until all hours in his home as well as his laboratory. In the 50 foot white mahogany den, a model of the first phonograph was examined. The original of this was loaned by Edison to the Kensington Museum in London in 1880. The story goes that an official of the museum when calling upon the inventor in his laboratory in Menlo Park, N. J. in 1880, asked Edison if he might take some remembrance of his visit back to the English museum as a loan. At the time Edison glanced around his laboratory and said, "Take that," waving to the original phonograph model. The museum kept this original for some years, being reluctant to release it. In fact it was not until Edison was given the Congressional Medal in 1928 that the Kensington Museum returned the original phonograph.



Fagus sylvatica pendula incisa (Large tree right of center) on the estate of Mr. and Mrs. Hendon Chubb, Llewellyn Park, West Orange, New Jersey

The Edison greenhouses were visited and then the gardens and grounds where special note was made of four Chinese chestnut trees (*Castanea mollissima*). Dr. A. H. Graves, our authority on the chestnut, had brought these trees as seedlings from his chestnut plantation in Hamden, Connecticut to Mrs. Edison. They are doing well and evidently blight resistant.

While visiting the stately gardens of Mr. and Mrs. Hendon Chubb, we saw their very fine cut-leaved European weeping beech (*Fagus sylvatica pendula incisa*), a tree estimated to be about 175 years old. The late Dr. Sargent pronounced it, to his knowledge, to be the largest tree of its kind in America thirty years ago. A photograph appeared in New Jersey Suburban Magazine (now discontinued) in 1931.

We enjoyed the spick and span appearance and the carefully controlled growing conditions of the orchid house as well as the garden at George Merck's estate and the Tilney gardens were fascinating. The dampening weather continued to quiet the birds and though we climbed the terraced garden way for a view from the hilltop it was mostly mist that we saw. However, we were reassured by the prospects for a repetition of the trip in 1952. Such trips are not common in our schedule of late and those interested in seeing these gardens and having an intimate sight of several nesting species of birds should plan to attend. Attendance 12. Leader, Gladys Gordon Fry.

August 25. Marine Park, Brooklyn, N. Y. Over sixty species of salt marsh, seaside, and weed plants were observed in flower. The sea lavender (*Limonium carolinianum*) and the glassworts (*Salicornia* spp.) were of particular interest in the wet salt marsh. After lunch and a short bus ride, the Crossbay Boulevard fresh water marsh in a salt marsh area was investigated. The marsh ferns (*Dryopteris Thelypteris*), the sphagnum moss, and the sundews (*Drosera rotundifolia*) in flower were found, but observed to be more crowded by higher growing plants than in previous visits. Attendance 12. Leader, Emanuel D. Rudolph.

September 2. Wolfe's Pond Park, Staten Island, N. Y. Due to heavy rain just before the start of the trip it was not advisable to get off the beaten path. Near Prince's Bay Station the group saw *Cedrus deodara*, *Cassia chamaecrista* and *Cassia marylandica*, *Cephalanthus occidentalis*, *Decodon verticillata*, *Celastris scadens*, *Diospyros virginiana* and *Ilex verticillata*. Near Hylan Boulevard was a large stand of *Lobelia cardinalis* in full bloom. Due to the wet weather the group decided to go to Great Kills Park to see shore birds. Among the common ones were also white-rumped sandpiper, willets, and northern phalarope. Attendance 12. Leader, Mathilde P. Weingartner.

September 16. Millneck, L. I., N. Y. The day was a perfect one as far as weather was concerned and we found many plants in bloom, among these were blue curls (*Trichostema*), golden aster (*Chrysopsis falcata*) and rough buttonweed (*Diodia teres*). The birds were plentiful with much evidence of migration going on. We had scarlet tanagers in the winter plumage; white-eyed, red-eyed, and yellow-throated vireos, warblers, several species of hawks and other migrants. There were three egrets in the pond and many yellow-legs and other shore birds on the small islands. It was a satisfying trip. Attendance 14. Leader, Farida A. Wiley.

September 16. Vicinity of Allaire State Park, N. J. Our field chairman, V. L. Frazee, told the history of the abandoned village of Allaire, a one-time iron smelting and manufacturing settlement. Mr. Frazee is a native of this region and recounted many interesting stories about James P. Allaire, Arthur Brisbane, and others. It is distressing, however, to see the damage done by vandals to the old buildings on account of insufficient policing. One wonders as to the wisdom of the State acquiring property when means are non-existant to protect, let alone to improve, it. A few new species of plants were added to the list and the autumnal flowers (*Solidago*, *Aster*, *Eupatorium* spp., etc.) of the park were examined. Some interesting ferns, lycopods, and coastal plain trees such as willow, holly, and magnolia were seen along the Manasquan river about one mile southwest of Farmingdale. The group then visited the nearby bridge over the Manasquan from which a large number of herbaceous and woody plants were observed on the July 29 trip (See Bulletin 78: 468 for that report). A final bit of botanizing near Mr. Frazee's home along the lower Manasquan included the salt marsh aspect. Attendance 15. Leaders, V. L. Frazee and Louis E. Hand.

September 29. Springdale, N. J. The joint fall meeting of the Torrey Botanical Club and the American Fern Society was held on September 29. The group met Dr. R. C. Benedict, the leader, at Springdale in Sussex County, N. J. This is one of the most beautiful sections of New Jersey with limestone outcroppings and cliffs dominating the landscape. We proceeded to the Whittingham Estate where we followed Dr. Benedict along a wood road to park the cars in the meadow near Big Spring. Here *Botrychium obliquum* and *B. dissectum* were found. Dr. Benedict then lead the way through the neighboring swamp to the place where sixteen years ago he had set out three heart's tongue ferns. One was found after some searching and was in good condition with several fruiting fronds. No sporelings were observed. Walking fern, wall rue and maidenhair spleenwort were found on the limestone outcroppings. After lunch at Big Spring we went to Andover where we were pleased to find the narrow-leaved spleenwort growing along the railroad right of way with *Pellaea atropurpurea* growing on the cliff nearby. Attendance 38. Leader, Dr. Ralph C. Benedict. Reported by W. D. Mann, Jr.

October 21. Bushkill Falls, Pa. It has been evident for some years that the liverworts and mosses of this region are varied and luxuriant; each visit reveals the presence of additional genera and lends assurance that trips to this area in future years will continue to be rewarding (See TORREYA 40: 175–177; 41: 136–137; 42: 141–142; 77: 141–142). Lichens are also common, and numerous forms were expertly identified by Mr. Nearing. The morning of this gray Sunday was spent mostly to the north and east of the main falls. *Diplophyllum*, *Scapania*, and *Microlepidozia* were still plentiful on the banks and slopes. Around the bases of the trees in the swamp beyond, *Tortella caespitosa* fruited abundantly. Higher up on the oaks *Frullania eboracensis* grew in profusion. Subsequent examination with the microscope revealed the presence of energetic rotifers in its ventral lobes, as Kerner had beautifully illustrated well over a half a century ago (NATURAL HISTORY OF PLANTS 2, p. 698). Both in the swamp and on the higher ground above, *Thelia asprella*, boasting new and carefully twisted snow-white peristomes, formed thick mats completely around the trunks of numerous trees. A search for *Buxbaumia* where it had previously been collected was in vain. However, *Leucobryum glaucum* was collected with numerous sporophytes sporting jaunty white calyptras; earlier in the day plants with masses of "radicular tomentum" has been observed. *Rhodobryum roseum*, *Mnium punctatum* var. *elatum*. *Fontinalis gigantea* and *Pallavicinia Lyellii* were found as in previous years, the last loaded with bulging perianths. Along the sides of the gorge, just above the main falls, maidenhair spleenwort, *Reboulia*, *Conocephalum* et al. were still abundant; *Geranium Robertianum* added a touch of color and of cheer to the ravine. On the rocky slopes opposite the main falls *Hylocomium proliferum* "fruiting" sparingly, lent its note of graciousness, while lower down on the banks *Trichocolea tomentella* replaced it, with *Metzgeria* as a neighbor. Less scrupulous collectors had apparently found "our" patch of *Woodsia ilvensis* near the top of the gorge. Later in the afternoon we travelled over the high ground to the tributary stream to the west. In the defunct ditch along the top of the ridge *Isopaches bicrenatus* flourished. It showed clusters of reddish gemmae, numerous perianths, and some open capsules, blissfully oblivious of the fact that, according to most authorities, these last are not scheduled to be present at this time of year. On the eastern slopes of this ravine *Porella platyphylloidea* grew on the stones, sharing one large rock with *Ulota americana*. The edge of the falls of this smaller stream contained mats of *Riccardia multifida*, *Pellia endiviaefolia* (*Fabroniana*) and *Jubula pennsylvanica*. In the adjacent springy bog there was also *Microlepidozia setacea*. As the gray of the sky deepened we found again, in this location, the rather bright yellow-green *Geocalyx graveolens*, and for the first time, the more yellow to brownish-green *Jungermannia lanceolata* with its stubby perianths. As we beat our way back through the brush, someone quoted, in paraphrase, "Hepaticis nox incubat atra." Attendance 17. Leader, Edwin B. Matzke.

November 4. Greenbrook Sanctuary, Alpine, N. J. The group first visited an experimental sphagnum bog which had been constructed. The bog, due to lack of water

and perhaps other factors, had begun to be invaded by grasses and sedges. The cattail was just beginning to grow in one end while several dry fruiting stalks of the Turks-cap lily were noticed nearby. The group proceeded from the bog to the northern end of the sanctuary through an area of severe storm damage (storm of Nov. 1950) and along the Fern Trail. There a Carolina or small-leaved maple (*Acer rubrum* var. *trilobum*) was seen. There was some speculation as to how this tree, common to the swamps of southern New Jersey might have become established in the sanctuary.

At the northern part of the sanctuary the group saw two great horned owls flush from their perch where these birds often take up their winter roost. Upon completing the loop around Owl Hill, the group returned to the Fern Trail, eventually crossing Green Brook and moving up its valley to Picture Point. After a brief glance at the Hudson and some taxonomy of oaks located at this point, the group continued on the Club Trail and stopped to examine a black oak (*Quercus velutina*) which harbored a growth of sweet knot (*Polyporus graveolens*), one of the few records of this fungus in the State of New Jersey. Attendance 17. Leader, Steven Collins.

November 11. Lakewood and Silverton, N. J. The upland pine barrens vegetation, a stream bank aspect, and a southern white cedar swamp were leisurely examined during the morning. Lunch was enjoyed under sunny skies and sheltered by the ever present pines. We then drove to the Silverton bog where nice stands of *Schizaea*, *Lycopodium carolinianum*, *Drosera filiformis*, and other bog species were seen without getting our feet too wet for the time of year. Some of the participants found this an ideal time for adding to their seed collections. Attendance 14. Leader, Eileen E. Hand.

November 18. High Point State Park, N. J. The final field trip for the year was conducted at High Point State Park, Sussex Co., New Jersey. The objectives of the trip were to visit the various plant communities and to note vegetational transitions correlated with soils and exposure.

The first stop was at the High Point Monument, 1803 ft. on the Kittatinny ridge, the highest point in New Jersey. Here the severity of the climate and its effects upon the vegetation were extremely striking. *Potentilla tridentata*, characteristic of alpine regions further north, was common in the rock crevices. A typical pitch pine—scrub oak community dominated the ridge top wherever the Shawangunk conglomerate was exposed by glacial scouring.

From the ridge, the group proceeded to Cedar Swamp. Here southern white cedar, a common coastal species, was found associated with hemlock and black spruce. The chestnut oak community was seen just above the swamp which finally gave way to an interesting talus where black and white birch were the characteristic species.

After lunch the members hiked down the southeast escarpment on the Appalachian Trail. A series of fascinating transitions were pointed out from the pitch pine of the ridge top to chestnut oak, oak-hickory, and finally hemlocks in the cove.

Upon returning we proceeded on a drive down through the Park noting old field succession, beaver activities, white oak community, and mixed hardwoods. Attendance 30. Leader, William A. Niering.

Book Reviews

Illustrated Flora of the Pacific States. Washington, Oregon, and California. By LeRoy Abrams. In four volumes, Volume III. Geraniaceae to Scrophulariaceae. 866 pp. illustrated, with index of genera and families. Stanford University Press, Stanford, Calif., 1951. $17.50.

The appearance in the late spring of volume III of this work planted another big milestone along the way of understanding the flora of the United States. It has been as eagerly awaited by those interested in the flora of the Pacific States as has its counterpart, the new Britton and Brown, by those in the Eastern States. The first volume, which

was planned to be the first of a three-volume work, appeared in 1923 and, following the Engler and Prantl system, covered the higher plants from ferns to birthworts. Volume II appeared in 1944 and included the buckwheats to the kramerias. It marked a new high in botanical illustration in American works of this scope. Volume III now continues the excellence of the preceding volume in format, typography, printing, stock, and binding and contains the treatment of all the families from the geraniums to the figworts. It is singularly free of errors, the most disturbing of the four detected being the transposition of Rhododendron legends on page 301. Volume I contains 557 pages, volume II, 635 pages, and volume III is up to 866 pages. Volume IV still must appear in order to complete this work, but manuscript for it is well advanced and, precluding delays in publishing which retarded both the second and third volumes, it should appear after a shorter interval.

Professor Abrams has been writing a superb flora. It is essentially complete in its coverage of the native flowering plants and ferns of Washington, Oregon, and California. These states have so great a diversity of climates, and consequently of plant life within their boundaries, that this flora is useful for identifying plants far beyond their limits. The synonymy and descriptions are very adequate, and the statements of range are satisfactorily definitive. In this connection it is satisfying to note the lack of annoying abbreviations so evident in some manuals. The classification is thorough and in accord with the great majority of present-day opinions.

The present volume treats some of the largest and most difficult families in the Pacific Coast region. Important portions of this volume, as in the earlier ones, have been contributed by specialists. Thus, to mention only the larger of such, I. L. Wiggins contributed the text for the Malvaceae, Cactaceae and Solanaceae, P. A. Munz the Onagraceae, Mildred E. Mathias and L. Constance the Umbellifere, H. L. Mason most of the Polemoniaceae, L. Constance the Hydrophyllaceae, and F. W. Pennell the bulk of the Scrophulariaceae. Dr. Abrams, with capable aid from Roxana S. Ferris and I. L. Wiggins, has done a splendid editorial job in keeping the treatments of all contributors uniform.

Many factors contribute to the satisfaction of users of this flora, not the least of which are the illustrations. The majority were the work of Jeanne Russell Janish, who has caught the essential features of her subjects so well that one can name the plant in hand without reference to the text.

Brewer and Watson's Flora of California and Gray's Synoptical Flora of North America were important standard works in the West for over half a century. We look forward to the completion of the Illustrated Flora of the Pacific States with the appearance of volume IV now in preparation, for it can safely be predicted that this work will dominate its field even more completely and for a longer time than the classics mentioned.—DAVID D. KECK, New York Botanical Garden.

Arizona Flora. By Thomas H. Kearney, Robert H. Peebles, and collaborators. viii + 1032 pages, with 32 unnumbered plates. University of California Press, Berkeley and Los Angeles, 1951. $7.50.

Arizona Flora is essentially a new work rather than a revision of U. S. Dept. Agr. Misc. Pub. 423, Flowering Plants and Ferns of Arizona.

This new flora adds one family, 32 genera, and 190 species that were not included in the 1942 book. Many of the ranges given are also more complete.

The authors are to be commended for delegating the work of preparing many genera or families to qualified specialists. Twenty-four of these collaborators are listed in the preface. Although they and the co-author have made valuable contributions to the flora, the book is essentially a monument to the diligence and genius of Dr. Kearney. Without his unceasing efforts the volume would not have been written.

The authors state that "The main objective of this work is to afford means for identifying the approximately 3,370 species of flowering plants, ferns, and fern allies known to be growing (or to have grown) without cultivation in the state of Arizona."

The policy adopted in Flowering Plants and Ferns of Arizona of giving various

"human interest" features of many of the plants has been continued. These features include such items as forage value and poisonous properties for livestock, food or mechanical value for humans, importance as hosts for insect or fungus pests, or value in Indian economy.

In addition to the keys and descriptions which comprise most of the work, 26 introductory pages discuss the botanical history and plant geography of the state. As a background for a detailed study of the vegetation of particular regions, the section on plant geography is an interesting and valuable feature of the text.

The following topics are covered in the first 26 pages:

"Introduction: botanical exploration" is an enumeration of the principal plant collectors in the state and a brief analysis of their collecting activities. "Part I: A Discussion of the Physical Background and Vegetation of Arizona," includes as subtopics topography, geology and soils, climate, vegetation in relation to physical conditions, and life forms. The discussion of these topics, each of which could involve one or more volumes on its own merits, is brief. Each does, however, fulfill its objective which is to introduce the reader to the topic.

"Part II: The Flora of Arizona" begins with a discussion of the plan of the book. This includes a section on the geographic elements of the flora of the state from point of view of origin or principal present distribution.

Thirty pages of excellent half-tones depicting plant communities or individual species add a decorative touch as well as portraying a few of the more unusual plants of the State.

Pages 27 through 971 constitute the main body of the work—the keys and descriptions. The 132 families and the genera belonging to each are described in the text; space did not permit a similar treatment of each species. As partial compensation, however, the descriptions in the keys are more complete than usual. The keys are the non-indented type. Although the authors realize that most botanists prefer the more easily-used indented keys, the non-indented form was adopted to save printing and proofreading expense.

The flora contains descriptions of the 132 families, 907 genera and 3,370 species of flowering plants, ferns and fern allies known to occur in the state. The ten largest families and the number of species in each, are as follows:

Compositae	543	Cyperaceae	100
Gramineae	369	Polygonaceae	94
Leguminoseae	287	Euphorbiaceae	84
Scrophulariaceae	112	Cactaceae	71
Cruciferae	105	Rosaceae	69

The portion devoted to descriptions and keys is followed by a list of 371 references to literature consulted and this in turn by a glossary and index.

The references are arranged in the same order they are referred to in the text rather than alphabetically. This makes it difficult to determine readily whether a given author's work has been included. An alphabetical listing would have been more convenient.

The glossary, which was lacking in Flowering Plants and Ferns of Arizona, will be a welcome addition to many. Beginners in systematic botany, in particular, found the lack of a glossary in the earlier work a distinct handicap.

The index in the new flora represents a marked improvement over the two indexes, one for common and one for scientific names, of the earlier work.

The entire book is executed with such painstaking attention to details that it sets a very high standard of accuracy for subsequent floras.—R. R. HUMPHREY, Department of Botany and Range Ecology, College of Agriculture, University of Arizona.

College Botany. Harry J. Fuller and Oswald Tippo. Henry Holt and Company, New York. 1949. xiv + 993 pp.

Textbooks of general botany continue to come—and go. This is one of the latest and apparently the most popular member of the family: a big book of nearly 1000 pages,

with the profusion of expensive illustrations (nearly 600) which none but university students can afford. It is a beautiful book, too, well printed on heavy paper, the figures of superb quality, the type large and easy to read, the terms printed in boldface to catch the drowsy eye. There is little that is new in the contents or in their arrangement. After a brief introduction, we find seventeen chapters on "the structure, physiology, and reproduction of flowering plants" (but is reproduction not physiology ?); then twelve chapters on "the plant kingdom"; and two final parts on "the distribution of plants in time and space" and "plants and man." The wide acceptance of the book must be based not on any novel matter nor on new perspectives in pedagogy, but on the way in which the matter is presented, the quality of the writing and of the illustration, the clarity and accuracy of the exposition.

Two widely divergent currents have been for some time evident in the teaching of botany in this country. One, recognizing that courses in "general botany" are not peopled entirely by incipient botanists, and professing certain views on the relation of science to a "liberal education," has tended away from detail, away from completeness, away from a complex terminology; the other, reminiscent of such classical texts as the old "Strasburger," and perhaps maintaining that professional botany is the only botany worth teaching, has insisted upon a more encyclopedic treatment. Fuller and Tippo belong to the latter trend. Their book makes full use of botanical terminology (there is a glossary of 733 terms); and there are few subjects in botany not at least touched upon, from the tetrakaidekahedral shape of cells to the phylogenetic relationships of the Sphenopsida.

In this age of showmanship and advertising it would perhaps be naive to expect that the tremendous task which the authors of such a work set themselves could be accomplished with the care and accuracy of earlier days. Even a rapid browsing of the book reveals numerous errors and inconsistencies. Inflorescences are so wrongly presented in all texts that it is not surprising to read (p. 448) that cymose types are "much less common than indeterminate inflorescences"; but this is not true. The treatment of fruits on p. 475 et seq. seems unnecessarily confused; the reader can never be sure just what the authors do mean by a fruit—whether simply the pericarp or the pericarp with other structures adhering; dandelion "seeds" and watermelons can scarcely exemplify "matured ovaries" as they seem to do here; and in the currently controversial status of the apple it is dangerous to identify the "core" (whatever that may be) with the "true fruit" (presumably the pericarp). In the account of heredity, the botanist will know that the authors did not really mean (p. 497) that the sizes of things are controlled "in most cases" by the environment and not by the inheritance; but students will think so. On the next page we read that each "trait" seems to be controlled by one gene; this is corrected seven pages later, but the student may not succeed in reconciling the two statements. Reference to the "union" of chromosomes (p. 502) may be misleading. The photograph of *Cornus florida* on p. 445 is turned on its side; and the figure on p. 656 of what is apparently an *Aspergillus* is mislabeled *Penicillium*. Parthenogenesis is wrongly defined on p. 471, correctly in the glossary; and the tube cell of pine does not "enter" (p. 821) the pollen tube. And so on and so on. Without doubt these things have all been corrected in later printings (which I have not seen). Perhaps they do not matter in teaching modern freshmen. And perhaps no one can any more write a textbook of botany which is free from them. However, it is perhaps worth noting that many of them are due to infelicity of expression and carelessness with words rather than to lack of information. (In compiling their glossary the authors ventured into the dangerous ground of etymology; with results which are often curious and occasionally startling.)

Since the popularity of this text cannot be due to authoritativeness, I concluded that its greatest attraction to botanists (if not to their students) might be the modern system of classification used. Most of the texts now available still arrange plants under such antiquated and discredited heads as "Thallophyta" and "Pteridophyta." Since our ideas of the larger groups of the plant kingdom have been rapidly changing, it is perhaps worth while to assess the modern contribution; this, in fact, is the chief excuse

for this review. Fuller and Tippo place plants in 12 phyla, arranged in the subkingdoms "Thallophyta" and "Embryophyta." (Such names are printed in quotation marks in the text to signify that they are "artificial group names"; see p. 529.) Seven of the phyla are "algae," one contains the bacteria, another the slime-molds, and one takes care of all the fungi proper; this disproportion surely reflects only the greater effort of recent algologists to reclassify and rename their larger groups, not a correspondingly greater homogeneity of the fungi. The Bryophyta form the eleventh phylum; and all vascular plants are placed together in the Tracheophyta. When we recall the difficulties in tracing relationships between lycopods and flowering plants (for instance), and the undoubted relationship between the bryophytes and the other archegoniates, such a disposition seems difficult to justify. And—most surprisingly in a scheme frankly labeled "the most nearly natural system of classification of living plants" (p. 35)—we still find that hoary myth, the Gymnospermae (not even printed in quotes) as a class within the subphylum Pteropsida. We have abandoned the Pteridophyta and Spermatophyta, having long since recognized that the relationships between ferns and cycads are closer than those between cycads and conifers; yet here is the same old error slipping in by the back door. It is curious to foist upon the beginning student a classification which at one end of the scale arranges plants in the greatest possible number of phyla and at the other end lumps them together to the point of fallacy. I called this a modern system; it might better be described as modernistic.

It is interesting to notice that of recently published textbooks of general botany, one other (by Robbins and Weier) has similarly divided the plant world into many "phyla"; vascular plants occupy four of these, the Psilophyta, Lycophyta, Sphenophyta, and Pterophyta, which correspond to the subphyla of Fuller and Tippo. If the distinct lines of "algae" are to be treated as phyla, then it would seem a good idea to do the same with vascular plants. The Gymnospermae are still there, however, in this treatment also, coordinate with the Filicineae and the Angiospermae under the Pterophyta. In fact, I have seen no textbook which ventures to discard this group into the rubbish-heap with "Thallophyta" and "Pteridophyta." Johansen, in a recent issue of *Chronica Botanica*, has proposed treating the "seed plants" under five heads: Pteridospermophyta, Cycadophyta, Ginkgophyta, Coniferophyta, Ephedrophyta, Anthophyta. This does for them what others have done for the algae, and by the use of such groupings it is possible to construct a classification which corresponds throughout with modern findings. Whether the names currently in use are usable is another matter. "Chlorophyta," used to replace the old "Chlorophyceae," unfortunately means "green plants" but does not include all green plants; "Chlorophycophyta" seems a frightful punishment for the inoffending freshman; "Pterophyta" is liable to confusion with the old "Pteridophyta," though used in a quite different sense. "Lycophyta" means "wolf-plants," "Pterophyta" means "wing-plants," "Lycopsida" means (if it means anything—the etymology is bad) "wolf-faces." The whole question of whether such names and such groups have a place in an elementary textbook is debatable; but if any part of such a system is to be introduced there, all of it should be.—H. W. RICKETT, The New York Botanical Garden.

Drawings of British Plants. By Stella Ross-Craig. Part IV. Resedaceae, Cistaceae, Violaceae, Polygalaceae, Frankeniaceae. *pl. 1–26.* 14 S 1950. Part V. Caryophyllaceae. *pl. 1–66.* 3 D 1951. London: G. Bell & Sons, Ltd.

Earlier parts of this series have been reviewed in the Bulletin (75: 672). The latest parts maintain the high quality of the first. The draughtsmanship, though somewhat metallic, is technically superb; and the profusion of detail drawn at high magnification should be of the greatest use in identification. Each part is indexed. Many of the species grow in the United States, and at the present low rate of exchange of the pound the work should be a real "buy" for Americans interested in plants; it costs less than three cents a plate.—H. W. RICKETT, The New York Botanical Garden.

Flowering Trees of the Caribbean. 30 paintings by Bernard and Harriet Pertchik. xii + 125 pages. Rinehart & Company, New York and Toronto. $10.00.

This book, measuring 9¼ by 12¼ inches, is striking in appearance, at least if the dust cover is retained. Opening it one wonders if this is the 20th century successor to the herbals. Here are full page color plates of each species, all arranged to occupy the right hand page. Several blank pages are thereby necessitated in the course of the book. Descriptive matter, folklore, and legends take up from two to four pages about each species. A scientific name and common names, sometimes from over twenty countries, are included and defined.

There is some uncertainty about the number of species included. The dust cover blurb calls for twenty-nine and lists that number while the title page proclaims thirty. Actually there are thirty, the first being only "a small shrub . . . has no true place in a book of flowering trees, but it is on the title page of this work to illustrate the way in which nature now and then mixes in a light touch of humor with its never-ending parade of beauty." The touch of humor here is the elf-faced flowers of *Ochna Mossambicensis*.

The paintings are assuredly the center of interest and importance. The Pertchiks were not botanists. A professional artist friend of the reviewer has pronounced the paintings as "photographic and unimaginative." To a botanist or to an amateur wishing to use the book to learn the plants, this will be considered complimentary to the artists. A photographic likeness is desired by such a person and artistic "imagination" may be misleading. The paintings differ from kodachrome reproductions in that the specimens, with the possible exception of *Couroupita guianensis*, are completely without any background to confuse the picture. Unless there be closely related species, one could surely identify these plants if found in bloom. This has been successfully tested by the reviewer on a recent visitor to the Caribbean.

It is clearly stated that "No single person is responsible for the finished book." The idea was apparently conceived by William C. White who has done the Introduction. Paul Knapp of the Alcoa Steamship Company did the text about each plant. In his quest for accuracy and for most typical specimens for the artists, Knapp was supported by personnel from many of the agricultural and other scientific institutions of the Caribbean as well as from the New York Botanical Garden and a taxonomist from Harvard University who is an authority on this flora. Few errors will be found though botanists may consider as rather free poetic license the statement (page 21) that in *Solanum macranthum*, "The corolla, sometimes three inches in diameter, is a single, rounded, flattish petal . . ." And the term "monopetalous corolla," used to describe *Napoleona Heudelotii* (page 24), was disapproved by Asa Gray in LESSONS IN BOTANY as early as 1887. If it be true that the fruiting branches of *Couroupita guianensis* "grow from the bark (originating from the axil leafbuds of the young tree), and curiously have no connection with the tree's wood . . ." this is amazing and one wonders how food and water are provided to the developing fruit.

Such a book could not be produced and sold for anything like $10.00 but for the fact that the art and engraving costs were borne by the Alcoa Steamship Company, holder of the copyright. But there is no "commercial" included and the company may well be commended for this support in extending the knowledge of Caribbean flora. The reader will also acquire a good deal of interesting historical information and folklore. There is a bibliography of 143 titles and a glossary.—JOHN A. SMALL, New Jersey College for Women, Rutgers University, The State University of New Jersey.

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INDEX TO AMERICAN BOTANICAL LITERATURE

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LAZELLA SCHWARTEN

WITH THE COLLABORATION OF THE EDITORS OF THE TAXONOMIC INDEX

TAXONOMY, PHYLOGENY AND FLORISTICS

ALGAE

(See also under Ecology and Plant Geography: **Chu & Tiffany**)

Blum, John L. Notes on Vaucheriaceae, with particular reference to western New York. Bull. Torrey Club **78**: 441–447. 14 N 1951.

Wohlschlag, Donald E. & Hasler, Arthur D. Some quantitative aspects of algal growth in Lake Mendota [Wisconsin]. Ecology **32**: 581–593. 5 N 1951.

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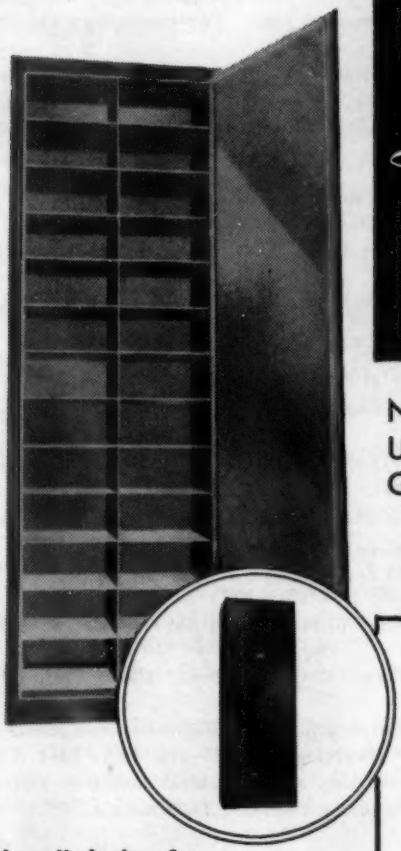

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